Biology and Ecology of Long Island Sound

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Chapter 6

BIOLOGY AND ECOLOGY OF LONG ISLAND SOUND

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6.1 Introduction

Long Island Sound (LIS) supports a wide variety of organisms whose distributions and abundances are controlled by processes operating at many spatial and temporal scales, from local habitat characteristics to long-distance transport of larvae. Ecological processes in LIS have been affected by natural and anthropogenic factors, including interannual variations in weather, commercial and recreational harvesting, eutrophication, nutrient-driven hypoxia, habitat degradation, and colonization by non-native species. Many of the most compelling management issues in LIS focus on how organisms respond to such stresses. In order to address these complex problems, we must first understand the factors controlling biological processes and how organisms interact ecologically. This chapter provides an overview of the major groups of organisms occupying the dominant habitats of LIS.

This chapter begins by describing the biota inhabiting the intertidal and shallow subtidal regions of LIS, including tidal marshes and submerged aquatic vegetation such as seagrasses, seaweeds, and benthic fauna. Next the subtidal and more open water reaches of LIS are discussed; separate sections on plankton, benthos, nekton, and other wildlife (birds, reptiles, and mammals) are included. We end this chapter by focusing on several ecological challenges to the biota of LIS, including hypoxia, introduction of non-native species, and climate change.

6.2 Littoral Zone: Habitats and Benthic Ecology

6.2.1 Intertidal Zone

Tidal amplitude ranges in LIS vary with time and location, ranging from ~0.75 to 2.2 m. LIS has a variety of littoral or intertidal habitats. These include rocky areas, cobble and sand beaches, sand and mud flats, and tidal marshes. Because of the interplay between the physiological stresses imposed by periodic aerial exposure and biological interactions related to competition and predation, many of these habitats are characterized by zones or bands in species distributions.

Physical factors play critical roles in structuring intertidal communities. Substrate type largely defines the dominant functional groups in the community. On consolidated substrates such as rock and large cobble, the substrate is stable enough to support attached organisms;

epiflora and epifauna tend to dominate. These include a variety of encrusting algae and seaweeds, sponges, mussels, snails, barnacles, and crabs. On mobile, unconsolidated sands and muds, the dominant organisms are inflora and infauna. Microalgae, various polychaetes, clams, and amphipods are typical of these habitats. Substrate stability is the critical factor, and for example, sand and mud occurring in protected, depositional environments can have substantial macroalgal cover.

The other physical factor is episodic disturbances created by ice, waves, sediment resuspension and transport, and burial under mats of wrack. Disturbances severe enough to kill organisms renew space and resources and permit species that are poor competitors to colonize (Rhoads et al. 1978). Recovery from the disturbance can occur by vegetative regrowth, seed germination, lateral growth or migration, and recruitment by seeds, spores, or larvae (Sousa 2001). The mode and rate of reestablishment depends on the disturbance characteristics, with low to moderate damage events tending to recover by vegetative regrowth and severe damage events by recruitment (Sousa 2001).

The most common intertidal habitats bordering LIS (including bays, harbors, and other sheltered areas) are salt marshes and shallow sloping intertidal flats (**Fig.** 1). Each represents about 31% of the LIS coastline. These are followed in importance by cobble, gravel, or riprap areas (19%), rocky intertidal (14%), and finally sand beaches (5%). The distribution of these habitats varies with region. Salt marshes (37%) are the most common habitat on the north shore of LIS while intertidal flats (51%) dominate the south shore of LIS. Both coasts have sizable amounts of exposed gravel, cobble, and riprap, but this habitat represents a large fraction (52%) of the eastern half of the Long Island shoreline. Overall, the south shore of LIS has about twice the amount of this habitat type as compared to the north shore. Although both shores have rocky areas, the natural areas tend to be exposed bedrock on the north shore and glacial erratics on the south shore.

6.2.2 Rocky Intertidal

The rocky intertidal (**Fig.** 2) has the most noticeable biotic zonation of all the intertidal habitats (Peterson 1991). This region is dominated by epiflora and epifauna living on the rock surfaces. Rock surfaces provide attachment sites, shelter in the form of crevices, and an attached source of microbial food. Physical factors such as desiccation, exposure to extreme winter and summer air temperatures, wave stress, and salinity stress are the strongest determinants of the upper limits of the distribution of organisms in this habitat, while biological factors tend to control the lower limits of their distribution (Berrill and Berrill 1981; Bertness et al. 2001).

Zonation in the rocky intertidal of LIS follows a pattern typical of the north Atlantic coast (Berrill and Berrill 1981; Bertness 1999; Nybakken 2001). At the highest level is the spray or splash zone; it lies above the spring high tide line and is dominated by lichens. Below that, in the region where only spring tides reach, is a zone where the rocks are black in color because of the presence of cyanobacteria. The most abundant animal in this zone is the rough periwinkle *Littorina saxatilus*. Within the high intertidal zone, which is inundated even during neap tides, the dominant animals are the northern rock barnacle *Semibalanus balanoides* and the common periwinkle *Littorina littorea*. Dominant species in the next intertidal zone are determined by the degree of wave action. On wave-exposed shores, the blue mussel *Mytilus edulis* is the most successful competitor in the mid-intertidal zone. On wave-protected coastlines, knotted wrack, *Ascophyllum nodosum,* and rockweeds *Fucus* spp., become the competitive dominants. Irish moss (*Chondrus crispus)* is the most abundant species in the low intertidal zone, generally below mean low water; this red alga is restricted to this zone because it can tolerate only short exposure times. Other common species include green algae such as sea lettuce, *Ulva lactuca*, and hollow green weeds, *Enteromorpha* spp., along with *L. littorea*. In the shallow subtidal, kelp such as *Laminaria saccharina*, and a variety of red seaweeds become abundant. On the surfaces of some of these, it is common to find the chink shell, *Lacuna vincta*. Throughout the intertidal zone, mobile predators such as the long-clawed hermit crab, *Pagurus longicarpus*, the rock crab, *Cancer irroratus*, the green crab, *Cancinus maenas*, the mud crab, *Dyspanopeus sayi*, and the Asian shore crab, *Hemigrapsus sanguineus*, play critical roles in regulating community structure.

The character of the rocky intertidal has changed over time as many key species have been introduced. These include, along with their approximate year of introduction, *H. sanguineus* (1992), *C. maenas* (1820s), *L. littorea* (1840s), and green fleece, *Codium fragile* (1950s) (Gerard et al. 1999, Steneck and Carlton 2001). It is likely that the rocky intertidal community during the 18th century bore little resemblance to that found in LIS today.

6.2.3 Gravel, Cobble, and Riprap

Organisms associated with unconsolidated, coarse-grained intertidal areas are regulated by the mobility of the substrate (**Fig.** 3) (Osman 1977; Sousa 1979). Large cobbles and riprap are resistant to movement and areas dominated by this substrate tend to resemble the rocky intertidal, with mid-tidal surfaces covered by *Semibalanus balanoides*), *Littorina littorea*, *Fucus* spp., and algal crusts (*Ralfsia* spp., *Hildenbrandtia prototypus*). As in the rocky intertidal, *Hemigrapsus sanguineus* has become a dominant predator in this habitat (Lohrer and Whitlatch 1997). Below this zone *Chondrus crispus* and *Codium fragile* are common (Hammerson 2004). Small cobbles and even smaller gravel particles are frequently overturned and shifted;

consequently, beaches with this substrate tend to resemble sandy beaches and have few species present.

6.2.4 Sand beaches

Sand beaches are common on the north shore of LIS (**Fig.** 4). They often appear barren but are populated by low numbers of large animals. Infauna predominate since the sand layer creates a buffer from temperature extremes and desiccation, and the substrate is too mobile to support attached plants and animals (Peterson 1991). Beach characteristics such as slope and particle size result from an interaction between wave action and source material (Nybakken 2001). In general, beaches that are coarser grained and more steeply sloped tend to drain once the tide recedes, while finer grained, gently sloping beaches retain water for longer periods of time after the tides withdraw. On a beach, sand grain size tends to be coarsest where waves break and becomes finer both towards the water and with increased elevation shoreward (Komar 1998). These grain-size variations contribute to biotic zonation (Peterson 1991), and generally more organisms are found on fine-grained beaches (Nybakken 2001).

The only primary producers on sand beaches are microflora such as benthic diatoms, since the sediments are too mobile for attachment of macrophytes (Nybakken 2001). The dominant fauna include suspension feeders, detritus feeders, and scavengers. Semi-terrestrial talitrid amphipods (e.g., *Orchestia grillus* and *Talorchestria* spp.) are found at or above the high tide level (Steinback 1999). Further down, the most common species include the isopods *Politolana* spp. and *Chiridotea* spp. at mid-tidal level, and haustoriid amphipods such as *Haustorius virginiana* and *Amphiporeia virginiana* and the spionid polychaete *Scolelepis squamata* in the swash or surf zone (Croker 1970; Weiss 1995). Some of the fauna, such as the talitrid amphipods, undergo fortnightly tidal migrations in order to maintain their positions relative to the wrack, (eelgrass, cordgrass, and macroalgae detritus) as it progressively moves up the beach (Steinback 1999). Wrack provides food, refuge, insulation against temperature extremes and desiccation, and breeding grounds for a variety of organisms, especially insects (Steinback 1999). Competition for space is not as intense as on rocky shores. In contrast to the slow predators in the rocky intertidal, the main predators on sand flats tend to be highly mobile fish, crabs, and shore birds (Peterson 1991). Characteristic birds include piping plovers (*Charadriud melodus*), least terns (*Sterna antillarum*), sandpipers (*Calidris alba*), ring-billed gulls (*Larus delawarensis*), and herring gulls (*Larus argentatus*) (Hammerson 2004; Weiss 1995). These birds feed on amphipods, polychaetes, and other invertebrates (Hammerson 2004).

6.2.5 Sand and Mud Flats

Sand and mud flats are found in depositional environments, in sheltered areas such as embayments and behind spits (**Fig.** 5) (Whitlatch 1982). These areas are often bordered by beaches and marshes landward and by eelgrass seaward. The principal producers are microalgae present as films or mats composed of diatoms, euglenoids, dinoflagellates, and cyanobacteria (Whitlatch 1982). Microalgae are often found in the upper intertidal but excluded from lower tidal levels by grazers like the mud snail *Ilyanassa obsoleta* (Whitlatch 1982). Macroalgae are generally rare because of the unstable nature of the sediments, but short-lived, highly productive macroalgae such as *Ulva lactuca* and *Enteromorpha* spp. sometimes become established for short periods of time (Whitlatch 1982).

Mud flats have similar dominant processes and tend to share fauna with fine-grained subtidal areas. The fine-grained sediments on mud flats retain water, have poor exchange with the overlying water, accumulate organic matter, and have high bacterial decomposition rates (Nybakken 2001). As a result, dissolved oxygen is usually only present in the first few mm of the sediment. Below that, pore waters are anoxic and rich in sulfides. Because mud flats are low energy areas, permanent burrows are possible (Nybakken 2001), so tube building invertebrates are common at mid-tidal levels. These include the surface deposit-feeding polychaetes *Polydora ligni* and *Streblospio benedicti* and the amphipod *Corophium* spp. (Whitlatch 1982). Other common surface deposit feeders include *Ilyanassa obsoleta*, the bivalve *Macoma balthica*, and the snail *Hydrobia truncata* (Whitlatch 1982). The principal suspension feeder at mid-tidal level is the soft shell clam *Mya arenaria*. This species forms an important commercial and recreational fishery in LIS. Burrowing fauna include the polychaetes *Lumbrineris tenuis* and *Heteromastus filiformis*. An important carnivore associated with mud flats is the polychaete *Nereis virens* (Whitlatch 1982).

Species zonation patterns are not very distinct but do occur on tidal sand flats, mainly due to physiological stresses associated with limited feeding and respiration times and biotic interactions such as predation and competition (Peterson 1991; Whitlatch 1982). Common molluscs include the predatory moon snail *Neverita duplicata* (=*Polinices*) and the small, suspension-feeding bivalve *Gemma gemma*. These tend to occur from the mid- to low-tide level (Whitlatch 1982). In the low intertidal zone, larger, suspension-feeding bivalves such as the common razor clam *Ensis directus* and the hard clam *Mercenaria mercenaria* occur. *Spiophanes bombyx* and *Arenicola marina* are representative deposit feeding polychaetes on sand flats. Both tend to be found at or above the mid-tide level (Anderson 1972; Whitlatch 1982). The former is a surface deposit feeder, and the latter builds a U-shaped burrow, funneling sediments to the mouth at one end of the burrow and defecating at the other. Horseshoe crabs (*Limulus* *polyphemus*) are a seasonal predator that digs pits on sand flats during high tide searching for invertebrate prey. They also spawn here in the high intertidal. Other predators utilizing sand flats include fish such as scup (*Stenotomus chrysops*), sand lance (*Ammodytes americanus*), and flounder (e.g., summer flounder *Paralichthys dentatus*) and a variety of birds, including sandpipers, least terns and gulls (Whitlatch 1982).

Reid et al. (1979) described a sand community distributed in shallow areas along the eastern two-thirds of Long Island, including the nearshore region in Smithtown Bay and from Port Jefferson to Mattituck Inlet. The molluscan fauna in this community was dominated by three suspension-feeding bivalves, *Ensis directus*, *Pandora gouldiana*, and *Spisula solidissima*, a surface deposit feeder *Tellina agilis*, and two gastropods, the suspension-feeding *Crepidula fornicata* and the scavenging *Ilyanassa trivittata*. Also abundant were two carnivores/omnivores, the painted worm *Nepthys picta* and *Pagurus longicarpus*, and a tubiculous, deposit-feeding amphipod *Ampelisca vadorum*. All stations with this faunal assemblage occurred at water depths less than 10 meters. This geographic region consists of a series of shoals whose major source of sand is from erosion of adjacent bluffs (Bokuniewicz and Tanski 1983). An accumulation of mollusc shells is generally present at the base of the shoals, and further seaward, the sediments become finer grained. Commercial harvesting of *S. solidissima* occurs on the shoals east of Mount Sinai Harbor.

In harbor areas, sand and mud faunal assemblages are affected by many of the same physical and biotic processes and are similar to assemblages found in the deeper subtidal areas of LIS. As a result, no separate discussion of these assemblages is necessary here. It is notable, however, that studies examining the structure of benthic communities in harbor areas tend to clearly identify community characteristics that suggest frequent natural and/or anthropogenic disturbances. For example, Ocean Surveys, Inc. (2010) found that a number of opportunistic species were abundant in Sheffield Harbor, Norwalk, CT. Cuomo and Zinn (1997) characterized the benthic community at most sites in the lower West River in New Haven and West Haven, CT as early to mid-successional (Stage I-Stage II, *sensu* Rhoads and Germano 1982) and suggested they were being maintained at that level by frequent disturbances. Cerrato and Lee (2008), in an investigation of Oyster Bay/Cold Spring Harbor, Huntington/Northport Bay, and Port Jefferson Harbor, found that portions of each area had benthic community characteristics that suggested the presence of stress. These included lower than expected species richness, anomalously low abundances, and dominance by low successional, opportunistic species. For example, in Oyster Bay/Cold Spring Harbor and Huntington/Northport Bay, more that 60% of all individuals collected belonged to one of five early successional species. Similarly stressed assemblages were found in Bowery Bay and Flushing Bay in the East River (Cerrato and Bokuniewicz (1986).

6.2.6 Tidal Marshes

Three broad classes of tidal marshes are present in LIS, salt marsh (polyhaline), brackish marsh (mesohaline & oligohaline) and fresh-tidal marsh (fresh). Salt marshes are the most common class near the shores of LIS. Each of these marsh types has characteristic plant and animal communities. Nichols (1920) describes the vegetation of the fresh, brackish and salt marsh “series”. For geological reasons, there are no extensive shallow waters, sheltered from wave action in LIS and so tidal marshes are small and the largest tidal marsh only 800 acres. Marsh acreage is estimated at 20,895 acres of tidal marsh with 84% in Connecticut. Prior to the passage of the CT tidal wetlands act in 1969, 30% of all tidal marshes were lost to unregulated activities such as filling, dredging and hydrological modifications (e.g., activities changing the natural ebb and flow of the tides, such as millpond dams and tide gates). Losses were greatest and least in the urban versus rural towns respectively. Passage of regulatory programs in 1969 in CT and 1973 in NY has largely arrested the loss of tidal marshes. A more complete description of the LIS marshes is found in the synthesis document entitled Tidal Marsh of Long Island Sound (Dreyer and Niering 1995).

Salt marshes (**Fig.** 6) are the most productive intertidal habitats in LIS. Two major trophic pathways occur in marshes. One is autotrophic, with phytoplankton and benthic algae at the base and suspension feeders and surface deposit feeders, respectively, at the second level. The other is detrital. The dominant salt marsh plants *Spartina* spp. are perennial, and during the fall they withdraw nutrients from the leaves and store them in roots and rhizomes. Leaves die back and over the winter are dislodged by ice and transported to the high intertidal. Mats of this decaying wrack can smother existing vegetation and eventually bare patches are opened up to new colonization (Bertness 2007). Once in the high intertidal zone, the plant detritus begins the long process of decay aided by physical fragmentation and microbial decomposition. This material represents the major food source for deposit feeders. Niering and Warren (1980) estimated that the production of above ground vegetation in the marshes of Long Island and Connecticut was about 93,000 metric tons per year.

Zonation in intertidal salt marshes is controlled by a combination of tidal flooding, salt stress, physical disturbances (ice damage, burial by wrack), competition, and predation (Bertness 2007). The low marsh, located between mean low and mean high water, is dominated by cordgrass (*Spartina alterniflora*). This salt tolerant plant forms a belt along the seaward edges of the marsh, with the tallest forms nearest the banks. The seaward colonization of cordgrass is limited by the degree of tidal flooding and its landward extent by competition with other plants. The high marsh extends from about mean high water to the highest spring tide level; this zone is only submerged during spring tides. The dominant plant is salt hay (*Spartina patens*), and it is joined by spike grass (*Distichlis spicata*), black grass (*Juncus gerardii*), and glasswort (*Salicornia* spp.). These high marsh plants generally outcompete cordgrass, but they are unable to successfully invade low marsh areas because they cannot tolerate the waterlogged soil there (Bertness 2007). Above the high marsh is an upland area that is exposed to seawater only during major storms. Major species in this zone include the marsh elder, *Iva frutescens*, and the red cedar (*Juniperus virginiana*). Recently, *Phragmites australis* has been displacing *Spartina* in salt marshes. Reasons for this are not completely understood but are probably connected to anthropogenic changes in the hydrologic cycle and nutrient inputs and the invasion of an aggressive subspecies (Chambers et al. 1999).

Prominent animals in salt marshes include ribbed mussels (*Geukensia demissa*), *Ilyanassa obsoleta*, and fiddler crabs (*Uca pugilator* and *Uca pugnax*). *G. demissa* is a suspension feeder found in the low marsh at the roots of *S. alterniflora*. *I. obsoleta* is a deposit-feeding snail that tends to occur in the low marsh and in mud flats adjacent to the marsh. The two species of fiddler crabs are deposit feeders and usually occur in the low marsh. *U. pugilator* is usually associated with sandy sediments and *U. pugnax* with muds. In addition, marshes are important areas for a variety of fish (e.g., the killifish *Fundulus heteroclitus*) and provide food, shelter, and nesting sites for birds such as herons and egrets (e.g., black-crowned night heron (*Nycticorax nycticorax*) and the snowy egret *Egretta thula*) (Bertness 2007).

The most familiar tidal marshes are the salt marshes with their characteristic short grassy meadows; the Wequetequock-Pawcatuck marshes of Stonington, CT have served as the paradigm for southern New England salt marshes (Miller and Egler 1950). Less common are the brackish meadows and brackish reed and fresh-tidal tall reed marshes. Nearly 30% of the Sound’s tidal wetlands are the fresh-tidal and brackish marshes of the Connecticut River and they constitute the best examples of in the northeast and were designated as Wetlands of International Importance under the Ramsar Convention in 1994. Details about these marshes are described in and are described Living Resources and Habitats of the Lower Connecticut River (Rozsa et al. 2001). Other small but noteworthy brackish marshes are the Quinnipiac, Housatonic (CT), Stratford (CT) and Nissequoque Rivers (NY). Plant (and rare plant) diversity is lowest in the salt marsh and highest in the fresh tidal marshes.

Tidal marshes provide extensive ecological services. Killifish (*Fundulus* spp.) consume marsh invertebrates such as amphipods, isopods and snails, foraging in the marshes during high tide and retreating to tidal creeks on the ebbing tide where they become prey for estuarine species such as bluefish, stripers and summer flounder. Marshes are habitat for birds, including the saltmarsh sparrow, which is considered globally vulnerable, and the seaside sparrow, which is also a nationally-ranked conservation priority. Both species inhabit the low grassy meadows of coastal tidal marshes. In the tall reed marshes will be found the secretive Least and American Bitterns. On the Connecticut River, the spring freshet floods the upstream freshwater tidal wetlands, which become natural impoundments at a time of waterfowl migration. The exemplary submerged aquatic vegetation of the tidal creeks and coves of brackish and fresh tidal marshes provide a refuge for migrating juvenile alewife and shad.

6.2.7 Science Gaps and Management Implications

Surprisingly little quantitative data are available on the spatial and temporal features of the intertidal flora and fauna, and the only shallow water data available are a small part of larger Sound-wide studies (e.g., Reid et al. 1979). As a result, most descriptions in this section relied on generic and/or decades old sources. It is safe to say that data and knowledge gaps on intertidal and shallow water biotic resources are so large that an accurate, reliable characterization cannot be made at this time. Even so, anthropogenic impacts are still clearly evident using simple measures such as the number of invasive species present, the fraction of marsh area lost, the amount of hardened shoreline present, or the obvious dominance of species that are advantaged by anthropogenic disturbances. The management implications of our current state of knowledge is that while the habitats can be identified and measured in extent, and while we have seen human-mediated change, what we have lost, whether we can recover any of it, and how we should proceed is largely unknown.

Virtually all of the tidal marshes have been ditched for mosquito control. Ditching in the early part of the last century was funded by coastal municipalities. Small unditched marshes occur but the two largest marshes are the Wheeler Wildlife Management Area in Milford, CT, and Great Meadows in Stratford, CT. The Connecticut Department of Health Services abandoned maintenance ditching in 1984 in favor of selective implementation of the more environmentally sound technique known as open marsh water management. This began a coast-wide experiment to determine how marshes might restore pool habitat and meandering tidal creeks. The unditched tidal marsh had extensive areas of shallow pools, which were an important habitat for shorebirds, wading birds and waterfowl.

The Connecticut Coastal Management Act of 1980 included a policy encouraging the restoration of degraded tidal wetlands and the Coastal Area Management Program began the systematic restoration of degraded tidal marshes. The primary restoration technique is to restore tidal flow by removing undersized culverts, tides gates and fill. Over 1100 acres have been restored in CT at more than 70 locations. Tidal marsh restoration in New York was delayed for the lack of a restoration policy.   The most remarkable restoration site is Fletchers Creek at Silver Sands State Park, Milford, CT, where tidal flow of an old municipal landfill was restored and several elevated areas were excavated.

Long-term studies of tidal marsh restoration have shown that tidal flow restoration causes a return of the pre-disturbance plant and animal communities. So salt marsh vegetation returns to former salt marshes but the elevation of degraded tidal marshes is typically lower than natural marshes. The dominant vegetation is therefore tall Spartina alterniflora and is thus a low marsh habitat. Hurricane Carol in 1954 destroyed the tide gates (which promote drainage and peat decomposition) at the Great Harbor Marsh (Guilford, CT), drowned the subsided marsh and created extensive peat flats. Over the next nearly 60 years, S. alterniflora had gradually colonized the peat flat in a downstream to upstream direction. The marsh above Great Harbor, known as Lost Lake, is still devoid of vegetation but the culvert under State Route 146 is undersized and impounds water in the tidal lake. High marsh has yet to return here. Elsewhere it has been shown (Warren et al. 2002) that marsh invertebrates return at various rates with the slowest being the salt marsh snail (Melampus bidentatus). It took 20 years for this snail to return to densities present at nearby natural reference marshes.

There are several non-native plant species in tidal marshes but the most notorious invader is the tall, woody common reed (Phragmites australis). This species does not invade salt marshes where the soil salinity is too high. However, upland salt marsh borders in contact with groundwater (i.e., brackish marsh communities) are a common place to find this invader. This is also the location of a natural disturbance where the highest spring tides deposit flotsam including the seeds and rhizome fragments of this grass. In contract, common reed colonizes the seaward edges of brackish reed marshes for the flotsam cannot penetrate the tall vegetation. Metzler and Rozsa (1987) surmised that common reed might be a non-native variety and that the diffuse form found at Great Meadows in Essex, CT, was the native form. Saltonstall (2002) used DNA analysis to demonstrate that the invasive form was from Europe and historic herbarium collections contained several native varieties to the U.S. The variety present at the Great Meadows in Essex has been determined to be the native variety and this may be the largest population in the northeast.

Tidal marshes are subject to loss due to several mechanisms. In the late 1980s, the Connecticut Coastal Management Program investigated a complaint of a dying marsh on the Five-mile River in Darien. It is was determined that the low marshes west of New Haven Harbor, on the north and south shore of the Sound are gradually subsiding and drowning. Over the course of two to three decades Spartina alterniflora undergoes a gradual but progressive stunting with the resulting habitat becoming an intertidal flat. Aerial photo and historic map analyses by Dr. Scott Warren at Connecticut College concluded that submergence began before the beginning of the last century. The cause of subsidence is unknown. Anisfeld and Hill (2011) dismissed nitrogen enrichment as a cause. Subsidence may have been due to the combination of tidal range and the acceleration of sea level rise in the mid-1800s. The most extensive submergence marsh in the LIS region is the brackish low marsh habitat of the

Quinnipiac River dominated by Typha latifolia (cat-tail). Several hundred acres have been lost since the early 1970s.

A rapid loss of Spartina alterniflora along creeks and mosquito ditch banks occurred in CT marshes beginning as late as 1999. This phenomenon has been termed sudden vegetation dieback and is found along the seaboard of the East and Gulf Coast states (Alber et al. 2008). The dieback is rapid, occurring in a single growing season and it is occurs simultaneously at multiple sites. The characteristics of this dieback suggest a pathogen, and the fungus Fusarium has been demonstrated to cause dieback in laboratory studies (Elmer and Marra 2011). The strain present in southern U.S. areas most closely matches a species from Africa and the northern species appears to be undescribed. Studies in the Caribbean have shown that various pathogens have been transported to the US in African dust. Dr. Wade Elmer at the Connecticut Agricultural Experiment Station continues to investigate this phenomenon. In CT, dieback is only associated with banks that are subject to daily tidal flooding and drainage at low tide. The stunted Spartina on ditch plugs is an indicator of the lack of drainage and these areas are unaffected by dieback. The discovery of root knot nematodes on Spartina is the likely cause of stress that triggers mortality when Fusarium is present. The combination of these two organisms is usually lethal for terrestrial crops.

The eroded edge (Miller and Egler 1950) is confined to the upland border of the salt marsh complex and impacts the high marsh community dominated by black grass (Juncus gerardii) and the rare coastal fen community dominated by switchgrass (Panicum virgatum). The edge resembles a pedestrian trail but forms on a 20-year cycle, which likely coincides with the lunar nodal or metonic cycle. Changes in the moon’s position cause the tidal range to predictably expand and contract which lead to peat building and then peat decomposition (‘erosion’). Following erosion, “forbs” colonize the barren areas and then are replaced by blackgrass (Juncus geradii) and then the erosion cycle begins. The next erosion cycle should occur around 2025.

6.3 Seagrasses and Seaweeds

6.3.1 Seagrasses

The two fully submerged estuarine vascular plants found in LIS are eelgrass (*Zostera marina* L.) and widgeon grass (*Ruppia maritima* L.). Eelgrass, the dominant seagrass in LIS, was once prevalent throughout the shallow coastal areas of LIS. Their Atlantic-wide die off in the 1930s resulted in the loss of eelgrass from much of the local area, but healthy populations were reestablished in eastern LIS by the 1950s. The recovery of eelgrass in western LIS was less successful and today those populations have all but vanished. Since the 1950s, eelgrass populations along the Connecticut coast have suffered additional losses thought to be linked to the effect of nitrogen loading on the coastal ecosystem. Additional losses are predicted to occur in response to rising sea levels, increases in storm activity, and increasing temperatures at temperate latitudes, all of which are predicted responses to climate change. Management of watershed activities and use of the coastal waters have the potential to mitigate the factors contributing to eelgrass decline. In addition, seagrass restoration efforts in the eastern LIS have been successful, indicating improving water quality in these areas.

6.3.1.1 Seagrass Ecosystem Services

Seagrass communities provide a range of ecosystem services (Hemminga and Duarte 2000; Orth et al. 2006). These communities provide foraging ground, shelter and act as a nursery to certain species of crustaceans, fish and mollusks (Beck et al. 2001; Heck Jr. et al. 2003; Orth et al. 2006). Seagrasses are considered ecosystem engineers; they change their environment, often to their own benefit (Bouma et al. 2005; Boer 2007). These changes include trapping of sediment resulting in increased water clarity (Bos et al. 2007). Additionally, these communities are effective at nutrient transformation, including substantial carbon sequestration in the sediment (Duarte et al. 2005; Romero et al. 2005; McGlathery et al. 2007). The major threats to seagrass communities are from human modification of the environment, specifically cultural eutrophication of coastal waters due to increased anthropogenic nutrient inputs (Short and Burdick 1996; Hauxwell et al. 2003; Orth et al. 2006; McGlathery et al. 2007; Waycott et al. 2009). Additional stressors to seagrasses include physical disturbance (boating, commercial fishing), disease and global climate change (Rasmussen 1977; Short et al. 1987; Walker et al. 1989; Short and Neckles 1999; Neckles et al. 2005). Seagrass communities are considered by some to be one of the most threatened habitats on the planet, but are often overlooked by the general public (Orth et al. 2006; Waycott et al. 2009).

6.3.1.2 Overview of Habitat Requirements

While many factors affect the success of seagrasses in the environment, light, nutrients and temperature influence these plants the most (Dennison et al. 1993; Lee et al. 2007). The distribution of *Zostera marina* and *Ruppia maritima* in coastal waters is also influenced by salinity, with *Z. marina* occurring in a more characteristically marine environment and *R. maritima* found in estuarine and freshwater areas (McRoy and McMillan 1977; Short et al. 2007).

Light is generally recognized as the limiting factor to which *Zostera marina* is most sensitive, having a high light requirement relative to macroalgae and phytoplankton (Dennison et al. 1993; Duarte 1995; Longstaff and Dennison 1999; Moore and Wetzel 2000; Hauxwell et al. 2003; Lee et al. 2007). Minimum light requirements of *Z. marina* range from 4% to 44% of surface irradiance, as amassed from review articles (Duarte 1991; Dennison et al. 1993; Batiuk et al. 2000) and experimental results (Dennison and Alberte 1985; Orth and Moore 1988; Olesen and Sand-Jensen 1993; Koch and Beer 1996). Minimum requirements determined for USA east coast populations range between 15% and 35% of surface irradiance, with studies specific to LIS and Massachusetts also falling within this same range (Dennison and Alberte 1985; Moore 1991; Koch and Beer 1996). The minimum light requirement is influenced by local conditions, including temperature, sediment and water column oxygen concentration, and sedimentary conditions (organic matter content and sulfide concentration). Under adverse conditions, the plants require more light. For example, temperature increases result in greater increases in respiratory rates relative to the concomitant increases in photosynthetic rates (Dennison 1987; Lee et al. 2007). In turn, the minimum light requirement is greater under higher temperatures to support productivity sufficient to meet the respiratory demands (Staehr and Borum 2011).

While the minimum light requirement varies with habitat conditions, a conservative estimate can be used to define a maximum depth limit for seagrass beds, based on the light attenuation coefficient (K_d) of the water. For areas with a relatively clear water column, eelgrass will colonize to deeper depths, while more turbid waters will restrict the eelgrass to shallower areas, which have sufficient light reaching the bottom to maintain the plants. The maximum depth limit under relatively ideal light conditions was calculated for LIS using the Lambert-Beer equation, following the method of Batiuk et al. (2000) for Chesapeake Bay. The maximum depth (z) was calculated using a minimum light requirement of 22% of surface irradiance (I_z/I_0) and a K_d of 0.7 m^{-1}:

$$z = \frac{ln\left(\frac{I_z}{I_0}\right)}{-k_d} = \frac{ln(0.22)}{-0.7} = 2.16\ m$$

Under current water quality conditions, the maximum depth limit for eelgrass in western LIS will be considerably shallower, given the greater light attenuation coefficients in the west. Values for K_d in eastern LIS are typically around 0.5 m^{-1}, yielding a predicted maximum depth of 3.1 m. In western LIS, K_d is closer to 1 m^{-1}, yielding a predicted maximum depth of 1.5 m, with an extreme of K_d reaching 4.4 m^{-1} (Koch and Beer 1996). The maximum distribution depth is further influenced by the tidal range (Koch and Beer 1996). In areas with higher tidal ranges, the light available at the bottom will be reduced at high tide relative to areas with lower tidal ranges, due to the greater amount of water through which the light must travel. Tidal ranges in LIS increase to the west, ranging from ~0.6 m in the east to ~2.5 m in the west. So, in reality, the maximum depth will be shallower in western LIS, given the greater tidal range and increased K_d.

Geographic distribution of eelgrass is also constrained by a minimum depth requirement and an apparent requirement for a minimum depth span between the shallow and deep edge of the bed. While some eelgrass is found in intertidal areas, eelgrass in LIS seems to require a minimum depth equivalent to half of the spring tidal range (Koch and Beer 1996), ranging from 0.5 m in eastern LIS to 1.25 m in western LIS. In addition to the minimum and maximum depth restrictions, modeling of depth distributions in LIS indicates these populations require a 1 m depth difference between the shallow and deep edge of the bed (Koch and Beer 1996). This vertical depth distribution requirement protects a bed from storm scour. Theoretically, the deep edge of the bed will be more resistant to storm scour, as the wave energy is attenuated with depth, thus providing a source population for recolonization of damaged areas. Under current K_d conditions, which serve to restrict the deep edge of the distribution, eelgrass is unlikely to survive in western LIS and is marginal in central LIS. These predictions match the current distribution of eelgrass (**Fig.** 7).

Nutrient limitation of eelgrass in natural environments is unlikely to occur as the plants have relatively low N and P requirements and have access to the nutrients in sediments via their root and rhizome network (Zimmerman et al. 1987; Lee et al. 2007). While sediment contains considerably richer concentrations of nutrients, assimilation of nutrients by leaves and roots can be nearly equal, with slightly more nutrients being assimilated by the roots (Lee et al. 2007). However, excess nutrients stimulate the growth of phytoplankton and macroalgae, both of which require considerably more nutrients than seagrass (Bintz et al. 2003; Hauxwell et al. 2003). Both phytoplankton and macroalgae have faster uptake rates of dissolved inorganic nitrogen and faster growth rates than seagrass (Duarte 1995). Thus the requirement for high light by seagrass also necessitates low nutrients in the water, or phytoplankton and macroalgae would flourish and shade the seagrass.

Zostera marina exhibits an optimal temperature range for growth with a worldwide average of 15.3ºC ± 1.6ºC and an optimal range for photosynthesis of 23.3ºC ± 2.5ºC (Lee et al. 2007). Above these ranges, the growth and photosynthetic capacity of *Z. marina* is reduced. In the shallow sub-embayments of LIS, summer temperatures often exceed 25^{o}C and may be detrimental to its success, inhibiting growth and possibly photosynthesis. Inhibition may result from thermal disruption of metabolic processes or from an increase in the minimum light requirement necessary to compensate for increasing respiratory demands (Staehr and Borum 2011). The higher mid-summer temperatures in LIS and its embayments lead to a bimodal growth pattern during the growing season of most years, with best growth in the spring and fall and inhibition in the warm summer months (Olesen and Sand-Jensen 1993; Moore et al. 1996; Bintz et al. 2003; Keser et al. 2003; Yarish et al. 2006). During the winter, production is almost nonexistent for *Z. marina* in LIS (Yarish et al. 2006).

6.3.1.3 Historical and Current Distribution

Zostera marina was common throughout LIS, within appropriate habitats, prior to 1930s. By the summer of 1931, most of the *Z. marina* ranging from North Carolina to New England and in much of the Atlantic had been wiped out by the wasting disease, attributed to the slime mold *Labyrinthula zosterae* (Short et al. 1987). Only an estimated 1% of the North Atlantic population remained, occurring primarily in the low salinity waters of upper estuarine areas (Cottam 1933). The eastern portion of LIS experienced a recovery by the 1950s, while recovery in western LIS was spotty and eventually failed (see references cited in: Rozsa 1994; Keser et al. 2003; Yarish et al. 2006; Johnson et al. 2007). In the 1990s, Clinton Harbor was the western-most location supporting *Z. marina (*Yarish et al. 2006*)*.

As part of the U.S. Fish and Wildlife Service's National Wetland Inventory Program, aerial surveys of eelgrass extent in LIS were conducted in 2002, 2006, and 2009 (Tiner et al. 2003, 2007; Tiner et al. 2010). These surveys were initiated with support from the Long Island Sound Study of the U. S. Environmental Protection Agency (EPA) and The State of Connecticut's Office of Long Island Sound Programs within the CT Department of Energy and the Environmental Protection (CTDEEP) (2002 and 2006 surveys). Continued support comes primarily from the Long Island Sound Study (2009 survey). These surveys indicate the majority of eelgrass acreage is found east of Rocky Neck State Park in Connecticut, and around Fisher's Island and Orient Point in New York (**Fig.** 7; Tiner et al. 2010, Pickerell unpublished data). A few beds still exist west of these locales. As of 2011, two small beds (2.6 ha total) of eelgrass were extant in the bight between Clinton Harbor and Westbrook Harbor associated with the Duck Island breakwater and a very small patch near the mouth of Clinton Harbor (Tiner et al. 2010; Vaudrey and Yarish unpublished data). Three beds (10 ha total) were identified along the North Shore of Long Island, but both the naturally occurring small patches and the restored areas at two locations were not identified as part of the aerial survey (Tiner et al. 2010; Pickerell unpublished data).

Aerial surveys of LIS are a critical tool for evaluating the long-term stability of eelgrass beds. Tiner et al. (2010) provide an analysis of the change in coverage of eelgrass among the three aerial surveys. At this point, the variability in bed area among the three surveys likely reflects interannual variability, a response to climatic and physical factors. The time series is not yet sufficiently long enough to detect long-term trends in eelgrass expansion or contraction. For example, the loss noted by the aerial surveys of 4.45 ha in Mumford Cove (Groton, CT) between 2002 and 2006 reflects the shifting of a sand bar in 2006, just prior to the survey. This shift resulted in the smothering of eelgrass in the southeastern portion of Mumford Cove. By the following year, eelgrass was once again growing in the denuded area (J. Vaudrey, unpublished data) and was reflected in the 2.8 ha increase noted between 2006 and 2009 surveys (Tiner et al. 2010). These small variations are in contrast to the longer history of eelgrass in Mumford Cove. Beginning in 1946, a wastewater treatment facility discharged effluent into the head of the Cove, from Fort Hill Brook (Vaudrey et al. 2010). Nutrient inputs increased until the outflow was relocated to the Thames River in October 1987. Water column nutrient concentrations decreased rapidly and by the following year, the recurring massive blooms of the green macroalga *Ulva lactuca* L. had disappeared. Recolonization of the Cove by eelgrass occurred slowly over the subsequent 15 years and has been relatively stable at ~20 ha since 2002 (Tiner et al. 2010; Vaudrey et al. 2010).

6.3.1.4 Linking Water Quality Parameters and Watershed Activities to Seagrass Distribution

Much of the research defining habitat requirement criteria for *Zostera marina* was conducted in the Chesapeake Bay area. Adequate light availability was identified as the most important criterion for seagrass with a number of secondary criteria and habitat constraints also playing a role in the presence or absence of *Z. marina* in a given area (Batiuk et al. 1992; Dennison et al. 1993). In the mid-1990s, Yarish et al. (2006) conducted a two-year study, in part to examine the habitat requirements for *Z. marina* in LIS. Ten years later, their suggested guidelines were applied to three case study sites to further evaluate suitability of the defined criteria in seagrass management along the Connecticut coastline (Vaudrey 2008a, 2008b). Results of these analyses suggest LIS seagrass requires more conservative standards, erring towards clearer water with less nutrient input relative to Chesapeake Bay (**Table** 1). Even more conservative standards are required when trying to establish a new bed in a site without eelgrass.

These studies verified the choice of habitat criteria limits by comparing field data for the parameters to the extant populations. For example, light attenuation coefficients in three eelgrass sites were compared to suggested criteria (**Fig.** 8). Eelgrass populations in Niantic River and at

Bushy Point are still viable, while the bed surveyed in Clinton Harbor between 1993 and 1995 has now disappeared (Yarish et al. 2006; Kremer et al. 2008). While the Clinton Harbor bed surveyed in the 1990s is gone, a small bed of eelgrass has been located in an area < 0.5 km away (Vaudrey and Yarish, unpublished data). Higher light attenuation coefficients, as seen in the Clinton site, may indicate eelgrass populations existing under stressful conditions (**Fig.** 8).

6.2.1.5 Current Trends in Seagrass Management

Management strategies in recent history have been shifting towards establishing criteria that are protective of key indicator species such as seagrass (Lewis III et al. 1998; Orth et al. 2002; Greening and Janicki 2006; Steward and Green 2007; Wazniak et al. 2007). Seagrass ecosystems have been described as “coastal canaries”, with the implication that loss of seagrass is a sign of degradation with associated loss of important ecosystem services (Orth et al. 2006). The benefit of managing for an indicator species (or habitats) versus setting a goal for a single parameter is the possibility of the inclusion of many factors that influence coastal waters, thus reflecting the diverse and complex interactions of these coastal communities. While many factors contribute to the success of seagrass, anthropogenic nitrogen delivered from watersheds has been identified as detrimental to seagrass. Latimer and Rego (2010) evaluated nitrogen load in relation to eelgrass extent in 62 Southern New England embayments, six in LIS. Results matched similar approaches applied to various seagrass species in embayments in CT, MA, FL, Australia and England (Short and Burdick 1996; Valiela and Cole 2002; Hauxwell et al. 2003; Steward and Green 2007; Vaudrey 2008b). Nitrogen loads below 50 kg N ha^{-1} y^{-1} were considered protective of eelgrass habitats, with variability in eelgrass extent attributable to other influencing factors.

Above 50 kg N ha^{-1} y^{-1}, eelgrass coverage was reduced and a complete loss of seagrass typically occurs above N loadings of 100 kg N ha^{-1} y^{-1} (Latimer and Rego 2010).

Connecticut's coastal management act (1980) does identify eelgrass as a coastal resource. Since the act provides protections to coastal resources and eelgrass is defined as a coastal resource, eelgrass is protected under that category. DEEP does consider eelgrass when reviewing and authorizing activities, such as dredging and construction of piers and docks. However, water quality criteria specific to eelgrass have not been adopted. While protections specific to seagrasses have not been adopted in Connecticut, but the potential adverse effect of land-derived nutrients on eelgrass communities has been recognized. Connecticut's management of nutrients in estuaries focuses on nitrogen reductions through the Long Island Sound Total Maximum Daily Load Analysis for dissolved oxygen (CTDEP / NYSDEC 2000). CTDEEP manages a number of nonpoint and point source programs designed to reduce nitrogen loadings to LIS. In addition to these programs and in order to more cost effectively achieve nitrogen reductions at wastewater treatment facilities, Connecticut implemented a nitrogen credit exchange (NCE) in 2002 (www.ct.gov/dep/nitrogencontrol). This approach has resulted in attainment of an aggregate nitrogen reduction limit from 79 wastewater treatment facilities located throughout the State. Further site-specific nitrogen reductions may be warranted to protect eelgrass via the restoration and maintenance of eelgrass habitat. CTDEEP continues to support the collection of information to further the scientific understanding regarding eelgrass habitat requirements and the impact of watershed loading on such requirements. CTDEEP will consider guidelines or standards as appropriate information becomes available.

As in Connecticut, protection of seagrasses in New York is somewhat limited in that there are no explicit protections afforded to eelgrass or widgeon grass. In order to address this deficiency, The New York State Legislature passed a law supporting creation of a Seagrass, Research, Monitoring and Restoration Task Force in 2006. The Task Force was charged with developing recommendations on elements of a seagrass management plan with the goal of preserving, restoring and mapping the native seagrass populations on Long Island. Additionally, the group was charged with recommending means of action that would bring about a lasting restoration of finfish, shellfish, crustaceans and waterfowl compatible with an improved quality of life and economic growth for the region (NYS Seagrass Task Force, 2009).

In response to the findings of the Seagrass Task Force (NYS Seagrass Task Force, 2009), members of the New York State Legislature drafted a bill to protect seagrasses in New York State waters in 2010. In June of 2010, the New York State Senate and Assembly passed the “Seagrass Protection Act”. Although there was no specific language as to how to achieve the proposed goals set forth in this bill, in principle it called for: (1) restrictions in the types of mechanically powered fishing gear used in seagrass meadows, (2) identifying pesticides and chemicals harmful to seagrasses and restricting their use near seagrasses, (3) restrictions on applying fertilizer containing phosphorus after November first and before April, and (4) development and adoption of seagrass management protective of both selected seagrass beds and traditional recreational activities. Some constituent communities expressed concerns about language within the bill and for this reason, the Governor did not sign the original bill and the law was never enacted. In 2011, a revised version of the bill was submitted to the House and Senate for a vote. As of July 2011, deliberation and voting on the bill had not yet commenced.

6.2.1.6 Restoration Efforts

The first documented eelgrass restoration attempts in the region were conducted in response to the catastrophic losses witnessed following the wasting disease outbreak of 1931 and 1932 (Cottam 1933). In what may be the first attempt to restore seagrass in the USA, eelgrass was transplanted at sites along the north mid Atlantic coast from Virginia to Massachusetts by the US Department of Agriculture, Bureau of Biological Survey and others during 1935 and 1936 (Lynch and Cottam 1937). As part of this effort “Pacific broad-leaved plants” collected in Friday Harbor, Washington and “Atlantic eelgrass” from Pungoteague Creek, Virginia and Mecox Bay, New York, were planted near Jones Beach, New York and in Great South Bay, New York in approximately 1 m^2 plots (Lynch and Cottam 1937). Additional work, although not well described in the available references, also involved the first documented use of seeds as a planting method for eelgrass. It appears that most of this work was unsuccessful, but it points to the fact that as early as the mid 1930s restoration was considered a worthwhile management tool.

Addy and Johnson (1947) reported on the results of several transplant attempts in Connecticut using eelgrass collected from a meadow in Niantic Harbor. Of the sites planted, Black Hall River (Old Lyme) and Hotchkiss Grove Beach (Branford) were reported as being “successful” while the Patagausett Cove (East Lyme) and Norwalk River (Norwalk) were not checked and failed, respectively. The only attempt made on Long Island, within Huntington Harbor, also failed. It was reported that wasting disease might have played a part in the demise of the Huntington Harbor transplants. By 1953 only the Hotchkiss Grove site still supported eelgrass and there is reason to believe that this same planting may have survived at least until ~1955. In 1955 and 1956 an additional planting was undertaken at the same site to either supplement what was already there or replace what had been lost. Anecdotal information indicates the planting of eelgrass in the Hotchkiss Grove site may have continued annually for thirty years (Rozsa 1994). The presence of this bed was confirmed in 1982 by staff of the National Marine Fisheries Service (Rozsa 1994). A subsequent survey by Yarish et al. (2006) from 1993 through 1995 did not locate this bed. However, the existence of live eelgrass at this site during 2010, and the lack of any proof of recent plantings, leads the authors to believe the plantings from the late 1940s, or at least the mid 1950s, may have persisted to this day (Vaudrey, pers. obs.).

Although there were several attempts to plant and restore eelgrass to NY waters in Peconic Estuary (PE) and the South Shore Estuary Reserve (SSER) beginning in the late 1970s and continuing in the 1990s, work in LIS did not begin until after 2000 (Churchill et al. 1978, Pickerell et al. 2007). In 2003, Cornell Cooperative Extension of Suffolk County (CCE) began test plantings in LIS near East Marion, NY. This work followed soon after discovery of healthy eelgrass meadows along the high-energy open coast on the east end of Long Island near Petty’s Bight (East Marion, NY) and Orient Point (Orient, NY). Detailed observations of these meadows lead to a better understanding of the type of habitats that were suited for the growth of eelgrass in LIS. Unexpectedly, these meadows appear to thrive in wave-swept and often high current areas in very coarse sediment composed of sand and gravel with large numbers of rocks and boulders. This extreme physical environment was a complete shift from the meadows known to exist historically throughout the PE and SSER, most of which occurred in fine-sediment dominated bottoms of protected bays, harbors and creeks. With this information, CCE staff set out to locate and screen suitable sites for eelgrass restoration potential along Long Island’s North Fork from Mattituck Inlet east to East Marion.

Using the reference meadows as a cue, the first pilot planting sites were chosen based on the conditions described above as well as their proximity to the eastern side of north facing points along the north fork: Terry's Point (Orient) and St. Thomas Point (Southold). This leeward location provided partial protection from northwest winds, the direction from which the most consistent and extreme fall and winter winds typically originate. This was important given that plantings were undertaken in the fall and shoots would not have time to root before the windy season began. Pilot-scale (i.e., several hundred shoots) plantings at both sites in 2003 resulted in healthy and expanding patches. Following this success, additional plantings were added during the second and third years at St. Thomas Point to create a very large and stable meadow (**Fig.** 9).

Additional projects were initiated to continue plantings further into LIS as far west as Lloyd's Neck (Huntington) and as far east as Plum Island (Southold) and Great Gull Island (Southold). The western plantings were intended to push the limits of eelgrass survival in the Sound and to test the interaction of planting depth, water clarity and tidal amplitude described by Koch and Beer (1996). Plantings at Lloyd's Neck were only partially successful and survival was limited to a very narrow band ~1m below MLLW. During the second growing season these otherwise healthy shoots were lost to erosion and it is not clear whether eelgrass can survive this far west in LIS based on water quality and tidal ranges.

At the time of this writing, the oldest restoration site on the north shore of Long Island has persisted for eight years. In total, eight successful planting sites run from Horton's Point (Southold) in the west to Great Gull Island (Southold) in the east and more work is underway to identify new planting sites and expand on the patches that have been created. Shoot densities at the oldest restoration sites compare favorably with reference sites and in fact, densities in portions of the restored meadows exceed the mean densities in the densest parts of the reference sites (Pickerell, pers. obs.) In July of 2011, within patch shoot densities at the Petty's Bight (East Marion) reference meadow were 513 ± 22 m^{-2} (mean ± standard error) while those at St. Thomas and Terry's Point were 401 ± 20 m^{-2} and 811m^{-2} ± 60 m^{-2}, respectively. In an attempt to apply the experience gained in NY to the CT coast, the latest round of restoration work applies methods used in NY waters to similar areas along the CT coast (Pickerell and Vaudrey 2010).

6.2.1.7 Science Gaps and Management Implications

In order to address the lack of estuary specific habitat criteria data for eelgrass in LIS, the New England Interstate Water Pollution Control Commission (NEIWPCC), with funding provided by US EPA is sponsoring a new research effort to develop a GIS-based model that will include those factors generally considered to be limiting to the growth of eelgrass in LIS (Pickerell et al. 2011). This project will: identify and map areas where eelgrass natural recruitment and/or restoration is possible; identify areas where restoration may be possible if water quality or other parameters improve; identify parameters limiting to eelgrass natural recruitment and/or restoration in areas determined to be unsuitable by the GIS model; and identity areas where eelgrass may colonize in response to sea level rise. This work is a collaborative effort between Cornell Cooperative Extension of Suffolk County, University of Connecticut and National Oceanic and Atmospheric Administration scientists and involves several of the authors of this chapter (Pickerell et al. 2011).

Seagrass beds constitute a vibrant and important community in LIS, providing habitat and food to a host of commercially and ecologically important species and serving as sinks for nutrients and suspended solids. Their presence indicates a desirable state of water quality, as the plants are adversely affected by high nutrient concentrations in the water column and the resulting issues often associated with high nitrogen inputs (e.g. algae blooms, hypoxia). The greatest threats to seagrasses in LIS have anthropogenic sources: cultural eutrophication and climate change. Continued monitoring of seagrass areal extent, density and metabolic parameters is key to understanding and predicting the response of seagrasses to a changing environment. Critical gaps in knowledge include an assessment of the current responses of LIS seagrass communities to locally occurring stresses (e.g. nutrients, temperature), and widespread data from LIS on the suitability of habitats for the support of eelgrass. An identification of seagrass communities exhibiting signs of stress would aid in focusing attention on locales most in need of management actions (e.g. nutrient load reductions, sediment load reductions, etc.). Habitat assessments could identify areas of LIS suitable for eelgrass restoration efforts. A combination of further research into metabolic responses of seagrass to stressors, appropriate management actions in coastal waters and watersheds, and continued restoration efforts will serve to preserve and perhaps expand the extent of eelgrass in LIS.

6.3.2 Seaweeds

LIS supports a very rich and diverse algal flora, with an estimated 250 species (Van Patten 2006; Schneider et al. 1979; J. Foertch, pers. comm. 2005). With a few exceptions, they are benthic, sessile species during the adult life stages, and inhabit the supralittoral, upper littoral, eulittoral, sublittoral, and subtidal zones on rocky shores of LIS. These algae have many diverse shapes and sizes; while some are perennial year-round residents, others may be annual or ephemeral. As is the case with most algae, species tend to have a highly “plastic morphology”, readily changing shape and color in response to environmental conditions such as light, temperature, photoperiod, substrate, wave action, and other parameters (Lobban and Harrison 1994; Lüning 1990).

6.3.2.1 Seasonal Cycles – Abundance and Biomass

The geographic location and orientation of LIS is such that it hosts an interesting and possibly unique assemblage of both cold- and warm-temperature tolerant species. Some of the Arctic-cold-to-temperate Atlantic assemblage includes species that originated in the Pacific and traveled to the Atlantic during Paleo-migration (Lüning 1990). There are also cold species that migrated south from Labrador and Greenland via the North Atlantic Boreal Current. These species tend to thrive in late fall, winter, and early spring. Using genetic analysis, Hu et al. (2010) postulated a trans-Atlantic repopulation of *Chondrus crispus* from localized refugia in Europe to North America following the Pleistocene glacial maximum, noting that its southern range seems to coincide with the 17°C isotherm described in Lüning (1990).

Saccharina latissima and *Saccharina longicruris* (kelp) are among the largest macroalgae species in the North Atlantic, and are key species supporting benthic communities. They are good examples of cold-water species at or near the southern limit of their biogeographic range. While these species are perennial in more northern locales, they are biennial in LIS. Late fall, winter, and spring are the best growth seasons; spring and fall are optimal for reproduction; and in the summer, abundance decreases as the water heats up, with blades degenerating in August (Egan and Yarish 1990; Egan and Yarish 1988; Van Patten and Yarish 1993; Yarish et al. 1980).

During the summer many warm temperate Atlantic species and even subtropical species appear, some of which may be endemic and others that travel north via the Gulf Stream. Subtidal examples include *Gracilaria tikvahiae*, several *Ceramium* spp., and *Champia parvula*.

In addition, there are of course a few invasive species from recent events (e.g. *Grateloupia turutura*, *Gracilaria vermiculophylla*, *Porphyra yezoensis*). The intertidal components of the Sound's marine flora are generally hardy perennial organisms which have adapted to extremes of temperature and light, particularly *Fucus vesiculosus* and *Ascophyllum nodosum*, which can be found year-round. *Ulva lactuca* (sea lettuce) can be found for most of the year in the upper littoral zone, but may bleach in very sunny weather (e.g., Pederson et al. 2008).

There are also several perrenating species which use two distinct morphologies as a way to cope with the extreme seasonal temperature ranges in LIS; for example, *Scytosiphon lomentaria* ("sausage weed"). This species puts out erect branching when temperature conditions are favorable, and becomes a small discoid crust when they are not (Lobban and Harrison 1994).

6.3.2.2 Distribution and Abundance

In general, the presence of macroalgae in LIS, like all photosynthetic organisms, is determined largely by the quantity and quality of light (e.g., Dring et al. 2001; Dring 1992) and thus is to be found in the photic zone; naturally requirements vary for individual species. In most estuaries, the successful species tend to be both euryhaline and eurythermic (Lee 1989). Wave action is also a significant factor in determining what grows where, and individual tolerances vary.

The historical, and also the current, challenge has been to establish what species are in LIS, in order to know how they may be interacting and changing. Initially, most work on the LIS macroalgae was taxonomic, with the intent of establishing a baseline of what species inhabited the estuary. Schneider et al. (1979) developed an annotated checklist of Connecticut seaweeds in 1979 for the Connecticut Geological and Natural History Survey. This is probably the last complete survey performed for LIS, although Dominion Nuclear’s Millstone Environmental Lab has done extensive continuous monitoring and surveying for the Eastern Connecticut shore of the Sound for the past three decades (e.g., Keser et al. 2010; Foertch et al. 2009). A University of Connecticut digital algal herbarium with many LIS specimens is available online at http://www.algae.uconn.edu.

Many macroalgae begin life as microscopic propagules in the water column that require hard benthic surfaces to settle on. Therefore the majority of species are found on rocky shores or where glacial cobble and till have accumulated. There are exceptions, such as some species that colonize mud flats and marshes (e.g. *Polysiphonia subtilissima*), or float (e.g. *Sargassum fluitans*). Algae tend to form distinctive bands or zones and develop specific morphological adaptations to cope with life on rocks, battered by wind and waves. These may include gripping structures, such as a holdfast, a crustose form, alternate life forms depending on seasons or conditions, and phycocolloids that act as both anti-desiccants and ”glue”.

Temperature, light and day length are primary factors controlling both distribution and productivity of seaweeds in LIS (Lee and Brinkhuis 1988; Brinkhuis et al. 1983; Yarish et al. 1984, 1986, 1987). Light intensity and wavelength are important for growth and reproduction. While individual species tolerances vary, the macroalgae can be grouped by the dominant photosynthetic pigments in their tissues, which accounts for the typical zonation of blue-green, green, brown and red algae as water depth increases. Light intensity decreases exponentially with depth, so macroalgae are constrained within the photic zone. Within the photic zone, temperature is generally the controlling factor for both intertidal and sublittoral distributions of algae in LIS (e.g. Yarish et al. 1984; Lüning 1990; Pedersen et al. 2008); other factors include exposure, nutrient availability, competition for substrate, and predation (Pedersen et al. 2008).

Few, if any, comprehensive studies of algal abundance and biomass for the entire LIS have been performed. Brinkhuis and colleagues examined 5 of the most common species in LIS–*Laminaria saccharina* (now *Saccharina longicruris*), *Gracilaria tikvahiae, Agardhiella subulata*, *Codium fragile*, and *Fucus vesiculosus*–for their potential as biofuels (Brinkhuis et al. 1982, 1983). Egan and Yarish (1988) described the geographic distribution of kelp on a large geographic scale, noting except for an outlier deep-water population of the coast of New Jersey, LIS is the southern limit for the species. Two species of *Saccharina* exist in LIS; one with a flat blade and long, hollow stipe (*S. longricruris*) and the other with a short, solid stipe and ruffled blade margins (*S. latissima*). Populations of *Laminaria saccharina* (now *S. longicruris and S. latissima*) were found at Black Ledge (Groton, CT) along the eastern Connecticut shore, and Cove Island, off Stamford Connecticut, and at several locations, such as Crane Neck and Eaton Neck, along the north shore of Long Island, and Montauk Point (Brinkhuis 1983; Egan et al. 1988, and others). Horsetail kelp, *Laminaria digitata*, was found at Montauk Point, New York and along the north shore of LIS from Groton, CT, and west to the Thimble Islands, Branford, Connecticut (Egan and Yarish 1988).

Most authors (e.g. Pederson et al. 2008) agree that for most of the year, the dominant algal species in LIS are: *Ulva* spp. (both tubular and sheet forming species) and *Blidingia minima* species in the upper littoral zone, Fucoids, particularly *Fucus vesiculosus*, in the mid-littoral, and *Chondrus crispus* in the infra-littoral and sublittoral. In a Cove Island study (Pederson et al. 2008), the invasive species *Codium fragile* periodically increased in abundance above the infra-littoral zone. Kelp were rarely recorded there. These authors also noted several species of *Porphyra* in the intertidal zone, but they were difficult to distinguish genetically and documenting the abundance was problematic for this genus, because of its morphology and epiphytic habit. Kim et al. (2009) noted that while most *Porphyras* occur seasonally, one, *Porphyra umbilicalis*, occurs year-round in the eulittoral zone. This species is the most abundant of the many *Porphyra* species in LIS (Yarish et al. 1998; Broom et al. 2002; Klein et al. 2003; He and Yarish 2006; Neefus et al. 2008). In the summer, these key species are still present, and *Scytosiphon lomentaria*, *Ceramium virgatum* and *rubrum*, and *Champia parvula* emerge. Few kelp are found below 5m depth (Egan and Yarish 1988; Yarish et al. 1990).

Eastern LIS monitoring by Dominion's Millstone Environmental Laboratory has been invaluable for demonstrating species diversity and abundance in areas both impacted and not impacted by the nuclear power plant's thermal plume. Recently use of multivariate analyses on the data has shed light on complex interactions at these monitored areas. The decline of *Chondrus* and *Fucus* in 1983, for example, with simultaneous increase in *Codium fragile,* has been correlated to the second cut for plume outflow made at Millstone. Subsequent recovery of *Fucus* has also been documented, and the post-*Chondrus* dominance of multiple species of red algae such as *Gelidium*, *Polysiphonia*, *Corallina,* and *Hypnea* has been correlated in Waterford to the addition of Dominion's Unit 3 (Foertch et al. 2009). This finding may provide insights into the potential effects of warming waters expected in the next decade and beyond (Keser et al. 2010).

Gerard (1995) observed shallow, hard-bottom algal communities at Crane Neck Point in central LIS and reported continuous dominance by ecologically and economically important species from 1983 to 1991. *Chondrus crispus*, called the "major groundcover", dominated the infralittoral to subtidal rock, with *Laminaria saccharina* (now known as *Saccharina latissima*) forming a canopy above it. She reported a dramatic change in community structure at this location in 1991, when kelp all but disappeared and *Chondrus* became sparse. Several species of finely branched red algae, i.e. *Cystoclonium purpurea* and *Phyllophora pseudoceranoides,* replaced *Chondrus*. *Punctaria latifolia* (a brown alga that resembles juvenile kelp blades), increased in abundance. This phenomenon lasted for about two years, after which *Chondrus* returned but kelp continued to be absent. The cause of the shift in species composition was arbitrarily attributed to a warm summer in 1991 and storm damage. This change was observed at other locations along the North Shore (Gerard 1995), while the Connecticut shore kelp seemed to be unaffected. Ecotypic differentiation in temperature tolerance in these populations might account for this phenomenon (Egan et al. 1990). Interestingly, Yarish et al. (1990) noted that sporophytes of *Laminaria (=Saccharina)* in western LIS, which routinely experienced warmer temperatures than eastern LIS kelp, did not exhibit greater survival at warm temperatures (20°C). However, there is evidence of genotypic differentiation of populations from the southern range of the distribution and those from mid range populations (Neefus et al. 1993). *Saccharina latissima* from LIS is exposed to higher summer temperatures and high nutrient regimes, and can tolerate more heat stress than the mid range type (Gerard and Du Bois 1988; Gerard et al. 1987). Meiospore germination and gametophyte growth at the southern boundary in LIS has been successful in July at temperatures as high as 25°C. Optimal growth temperatures for gametophytes shift from 10-15°C in March to 15-20°C in July, exhibiting patterns of seasonal temperature acclimation. Optimal growth of young sporophytes for the species is 10-15°C all year, but sporophytes from LIS have been found to survive up to 20°C for all months except January (Egan et al. 1989; Lee and Brinkhuis 1988; Egan et al. 1990). The survival of plants in LIS at higher temperatures is attributed to the ability to accumulate and store higher levels of nitrogen in their tissues. The additional nitrogen reserve bolsters the photosynthetic apparatus and possibly contributes to production of protective heat shock proteins (Gerard 1997).

Of course, temperature is not always the primary factor affecting distribution. Kim et al. (2008, 2009), in studies of *Porphya* species at different tidal elevations, found a correlation between nitrate uptake (which may be enhanced by desiccation) and vertical distribution patterns.

So far this discussion has focused on hard-bottom algae, but there are estuarine soft-bottom species such as *Polysiphonia subtilissima*, *Bostrichyia radicans*, *Caloglossa leprieurii* and *Neosiphonia harveyi* that commonly grow at the base of *Spartina alterniflora* in shallow embayments, salt marshes and muddy areas of LIS. These epiphytic, finely branched rhodophytes use the marsh vegetation for support and shade (Yarish and Edwards 1982; Yarish and Baillie 1989).

6.3.2.3 Productivity

No comprehensive quantitative assessment has been made to our knowledge of the overall productivity of LIS macroalgae, but some studies estimated productivity via measuring biomass at specific sites. Field and laboratory studies by Egan and Yarish (1990) show that *Laminaria/Saccharina* kelp is the most productive of the LIS macroalgae due to large size and rapid growth. At Flax Pond on the north shore of Long Island, Brinkhuis (1983) found that salt marsh *Ascophyllum* produced about 600 g (dry wt) m^{-2} y^{-1}.

A Gas Research Institute and General Electric-sponsored biofuel study (Brinkhuis et al. 1983) involved growing five common LIS species in culture and comparing biomass and growth rates. This resulted in the recommendation of *Laminaria saccharina* (now *Saccharina latissima*), as a biomass candidate. This was primarily due to its superior growth and productivity during the winter months. *Gracilaria tikvahiae*, a warm water species, was also suggested as a candidate because of its high productivity during May to October. *Aghardiella subulata*, *Codium fragile*, and *Fucus vesiculosus* were additional possible candidates. Productivity by *Codium fragile* was similar to *Fucus* and *Laminaria* under these study conditions. *Ascophyllum*, *Palmaria*, and *Ulva* were ruled out. This study never made it to commercial production because, while feasible, it was not economically advantageous at the time.

Some studies (Gerard 1999) showed an interesting relationship between *Spartina alterniflora* (salt marsh cordgrass) and *Ascophyllum nodosum* (bladder wrack). On southern New England, mid-Atlantic coasts, these species were mutually beneficial and the combination of the vascular and non-vascular species resulted in high productivity for the marsh-estuarine system. It was thought that the cordgrass offered some shade to help with desiccation issues for the *Ascophyllum*, while a decaying layer beneath the mat of *Ascophyllum* provided nutrients for *Spartina* (Brinkhuis 1976).

6.3.2.4 Trophic Interactions

As the base of the food chain, macroalgae directly and indirectly provide sustenance as well as habitat to a variety of animals–and humans (Lembi and Waaland 2007). For human use, kelp is used to make soup stock, or “dashi”, and also eaten whole as a sea vegetable, or by pickling sections of the stipe as “sea pickles.” It is also traditionally liquefied for use as a fertilizer in gardens (Chapman and Chapman 1980). Commercial cultivation or harvesting is not done in LIS as it is in many Asian and European nations, but individuals still gather and use the bounty from the shore. *Chondrus* is collected and used mostly to make traditional blanc mange pudding, or to thicken stews. *Palmaria palmaria* (“dulse”) is dried and eaten as a snack or in various recipes; *Ulva* (tubular species) is used in “seaweed salad”, and *Fucus vesiculosus* is used in the traditional New England clambake or brewed for tea. One additional human food that should be mentioned is *Porphyra*. Dried blades are flaked and used as a condiment. Certain species are gathered and pressed into sheets as nori to make sushi wrappers, but while this had been done commercially in Maine, it is presently not done in LIS or the Gulf of Maine (Chopin et al. 1999; Chopin et al. 2001; He and Yarish 2006; Pereira and Yarish 2010; Yarish et al. 1999).

Aside from human consumption, there are herbivorous predators of these primary producers in various sizes and types. Finfish, gastropod snails and sea urchins are key consumers of macroalgae. The trophic relationship between kelp and urchins such as *Strongylocentrotus purpuratus* is well known (e.g., Vadas 1977), and the gastropod *Lacuna vincta* is a voracious predator of kelp (Egan and Yarish 1990). Gastropods such as *Littorina* spp. feed on fleshy (*Ulva* spp.) and even crustose algae such as *Ralfsia verrucosa*. Mesograzers such as copepods, amphipods, and polychaetes are less studied but important grazers of macroalgae (Lobban and Harrison 1994).

However, in most situations, less than 20% of the algal biomass consumed passes through herbivores; a greater amount becomes part of the detrital food web (Vadas 1985).

A study conducted at Avery Point examined mutually beneficial relationships between snails and their seaweed hosts (Stachowicz and Whitlatch 2005). Results showed that *Chondrus crispus* had greater abundance and far less fouling from ascidians when two common snails, *Anachis lafresnayi* and *Mitrella lunata*, were present than when they were absent. This indicates that the snails were feeding on the tunicates attached to *Chondrus* rather than the *Chondrus* itself, to the benefit of both.

Historical anecdotal reports praise *Gracilaria tikvahiae and Agardhiella* as settlement surfaces for scallops in Niantic Bay and other locations (e.g. Goldberg et al. 2000). They are frequently found together, and observations that *Gracilaria* also tended to occur in hypoxic areas may be a reflection of its ability to take up nitrogen effectively.

Due to high balanced levels of protein, lipid, and carbohydrate, several of the common LIS algae have been used in aquaculture as nutrition for animals. A study at the National University of Galway (then University College Galway) showed that abalone preferred *Palmaria palmata* in their diets, and that a mixed diet of *Palmaria* and *Laminaria* provided the best nutrition for these mollusks (Mai et al. 1992). Much remains to be further investigated in terms of trophic transfer from algae.

6.3.2.5 Human Impacts

In an environmental contamination study, Shimshock et al. (1992) found that kelp from LIS near the Thames River in 1986 contained high levels of metals such as copper and cadmium, particularly in older blades and stipes. The authors observed that the ability of these algae to concentrate trace metals from the surrounding water suggests their use for biomonitoring.

In addition to indicating potential environmental problems, macroalgae can also assist in diminishing the impact of man. *Porphyra* species have been investigated for their potential as nitrogen scrubbers in nutrient bioremediation (e.g., Chopin et al. 1999; Carmona et al. 2001; Chopin et al. 2001; McVey et al. 2002) and two native Sound species were deemed suitable for integrated multi-trophic aquaculture and bioremediation (Yarish et al. 1999; He and Yarish 2006).

Some threats are harder to document or observe. Van Patten et al. (1993), in a study of the effects of temperature change on reproduction of kelp, pointed out that LIS kelp, at its southern limit, could be eliminated by a warming of 1-2° C. Reproductive effort in LIS was considerably less than that of kelp in New Hampshire or Nova Scotia. Davison et al. (2007) demonstrated in the laboratory that the interactions between nitrogen metabolism in Atlantic *Laminaria saccharina* and ultraviolet radiation are very complex, and need to be considered when evaluating the effects of anthropogenically increased UV on ocean productivity.

As climate change proceeds, increasing ocean acidification from carbon dioxide may particularly affect calcified species such as *Corallina officinalis,* due to the solubility of their high-magnesium calcite skeletons (Hall-Spencer 2008). Corallinas are found in rocky habitats, and are epiphytic on seagrass (Hemminga and Duarte 2000). Acidification may lead to profound changes in the food webs and diversity of seagrass meadows (Martin et al. 2008), because epiphytic coralline algae are primary colonizers of seagrass, and are subsequently followed by many other species such as diatoms, sponges, foraminifera, worms, and other invertebrates (Corlett and Jones 2007). Bussell et al. (2007) found 125 species of invertebrates in communities associated with *Corallina officinalis* in a United Kingdom study, illustrating the richness of these associations. Martin et al. (2008) concluded that by the year 2100, calcium carbonate production by coralline algae could decrease by 50%, with large consequences for local sediment budgets and biogeochemical cycles of carbon and carbonate in shallow coastal ecosystems.

Another human impact seen all too often is that of invasive species. Such species are frequently introduced by human activities, e.g. the introduction of *Codium fragile* ssp. *tomentosoides* to the East Coast of North America in 1957 (Bouck and Morgan 1957) or earlier

(Provan et al. 2007) probably via shipments of shellfish and ship hull transport (Carlton and Scanlon 1985). This highly invasive, buoyant species disrupts shellfish beds. Baitworms have been suggested as another, modern vector for distributing invasive species (Yarish et al. 2010).

A globally spreading, large invasive red seaweed from Asia, *Grateloupia turuturu*, was first identified in LIS in 2004 (Millstone Environmental Laboratory, 2009). A large, multi-state, multi-investigator Sea Grant study investigated the impacts and spread of this newcomer, which is well established at Millstone Point in Waterford Connecticut and as far east as Groton, CT. Although *Chondrus crispus*, a competitor for habitat, is holding its own so far, future warming of LIS may facilitate the spread of *Grateloupia* and it may outcompete native species (Yarish et al., 2010). The same study showed that *Grateloupia* was not a preferred food item for most herbivores, and that it grows quickly so could become dominant and change community structures. It reproduces well (Lin et al. in prep.) but decomposes quickly and so is a poor source of food to surrounding systems (Janiak 2010). While there are good efforts at educating the public about the control of invasive species, more education and more vigilance will be important for the future.

Several new invasive species in the genera *Porphyra* have been found in LIS since attention turned to it in the late 1990s as an economically important genus for the commercial sushi trade and other industries. Species were identified and described using DNA analyses (e.g. Broom et al. 2002; Klein et al. 2002; Neefus et al. 2000; Neefus et al. 2008). Very recently, Nettleton et al. (2012, in prep.) found, by means of molecular screening, that the invasive alga *Gracilaria vermiculophylla* is in LIS. It has apparently gone undetected for years, because it so closely resembles a related native species. This underscores the importance of DNA sequencing in future monitoring efforts.

In a Sea Grant-funded study of bait worm packaging as a potential vector of invasive species transport (Haska et al. 2012), investigators found that the seaweed packing (*Ascophyllum nodosum*) and baitworms yielded unintentional “stowaway” species. Microscopic examination and DNA analyses of purchased bait box contents yielded 13 species of macroalgae and 23 species of invertebrates. Two species of microalgae that are considered to be potentially toxic in bloom conditions, Alexandrium fundyense and Pseudonitzchia multiseries, were detected. This underscores the need for consideration of alternate packing materials or education on proper disposal methods of the seaweed packing used in bait boxes.

Finally, the careful records kept by the Millstone Environmental Laboratory (Keser et al. 2010) are insightful for suggesting what species of algae may become dominant in LIS with continued warming. We may expect a shift from kelp and other brown intertidal algae to more warm temperate branched red algae such as *Gracilaria tikvahiae* and even the invasive species of *Grateloupia turuturu* and recently discovered *Gracilaria vermiculophylla* with further warming.

6.3.2.6 Science Gaps and Management Implications

Brodie et al. (2009) pointed out that there are endangered algal species and even species that have become extinct. So little monitoring of the seaweeds is done at present that we might not even know whether important species are in serious decline. Brodie and co-workers summed it up by saying that “For the marine macroalgae, evidence of the impact of climate change, ocean acidification and introduced species on native floras is often anecdotal and points to the need for long-term monitoring and scientific study to determine changes in abundance and distribution”.

In the future, the use of macroalgae in integrated multitrophic aquaculture and bioremediation will need to grow. In addition, given the global spread of invasive species and the uncertainties associated with large-scale ecosystem changes due to global warming, it will be essential to develop additional monitoring efforts and habitat surveys to have a basic understanding about what large- and small-scale ecological changes are happening in communities that depend on the macroalgae. If this doesn't happen, the old saying "You don't know what you've got till it's gone" could turn out to be true in the case of some valuable seaweeds and the fauna that depend on them.

6.4 Plankton

The earliest plankton studies in LIS date back 70 years with the first estimates of primary production (Riley 1941). During the 1950s a series of studies on species composition and abundance of phytoplankton (Conover 1956), zooplankton (Deevey 1956) and primary production (Riley 1956) were carried out. During the 1980s, a series of studies measured micro- (Capriulo and Carpenter 1980) and mesozooplankton grazing (Dam Guerrero 1989, Dam and Peterson 1991 & 1993), and copepod phenology (Peterson 1986) and copepod egg production (Peterson and Bellantoni 1987). Starting in the 1990s, a more comprehensive spatial examination of plankton biomass and abundance took place (Capriulo et al. 2002), and has continued thanks to the Connecticut DEEP water quality monitoring program (Kaputa and Olson 2000; Dam et al. 2010). The program, with about 20 stations sampled at least at monthly intervals, covers the entire Sound. Monitoring programs for phytoplankton (Liu and Lin 2008) and zooplankton (Dam and McManus 2009), albeit at fewer stations, from the CT DEEP started during the first decade of the 21st century. Spatial studies of primary production were carried out in the first decade of the 21st century (Gobler et al. 2006; Goebel et al. 2006).

Here, we summarize information on both spatial and temporal patterns of phytoplankton and zooplankton in Long Island Sound. We also examine primary production and its fate. Emphasis is placed on new information available since the review by Capriulo et al. (2002). In the analysis, we take advantage of the extensive spatial coverage of the LIS Study (1988-1989) and of the water quality monitoring program of CT DEEP (since 1991).

6.4.1 Phytoplankton

The seasonal cycle of phytoplankton in LIS was first studied in the early 1950s (Conover 1956). In that study, and subsequent ones in the 1980s (Peterson 1986; Dam and Peterson 1991; Dam et al. 1994), sampling was done in central LIS and only for a few seasons. However, because there is a strong population gradient from west to east along the shores of the Sound, there is also a concomitant gradient in nutrient loading, plankton biomass and primary production (Bowman 1977; Wolfe et al. 1991; Lee and Lwiza 2008; Gobel et al. 2006). The first comprehensive spatial study in the Sound took place in the early 1990s: three nearshore stations that covered the eastern, central and western LIS were sampled at monthly intervals for a period of three years (Capriulo et al. 2002).

6.4.1.1 Temporal and Spatial Patterns of Chlorophyll

The most comprehensive spatial study of LIS to date has been carried out by the CT DEEP monitoring program since 1991. About twenty stations that cover the entire area of the Sound are sampled monthly throughout the year, or biweekly during the summer. The program divides the Sound into five regions, from west to east (**Fig.** 10): The West Narrows, the East

Narrows, the West Basin, the Central Basin and the East Basin (Kaputa and Olson 2000). Figures 11 and 12 show, respectively, time series of dissolved inorganic nitrogen (DIN) and chlorophyll at the extreme ends of the Sound-- the West Narrows and the East Basin. During the 1988-2005 period, means of both annual and DIN and chlorophyll were consistently higher, by a factor of 3-5, in the West Narrows than in the East Basin (Dam et al. 2010). During that period DIN concentrations were significantly greater in the West Narrows than in the Central and East Basins (Dam et al. 2010). Chlorophyll concentrations were significantly greater in the West Narrows than all other regions during some years, but during other years chlorophyll concentration in the West Narrows was only greater than in the East Basin (Dam et al. 2010). In summary, there is indeed a dramatic decrease in nutrients and phytoplankton biomass from west to east in LIS, but this decrease is not monotonic. That is, most of the spatial differences among regions occur between the extreme ends of the Sound, the Narrows and the East Basin.

LIS also displays both seasonal and long-term patterns in phytoplankton biomass and nutrient concentrations (Figs. 11, 12). The seasonal pattern is characterized by a chlorophyll maximum in late winter or early spring. A smaller chlorophyll peak occurs in early fall. Chlorophyll decreases during the summer, when nutrients are dramatically drawn down (Riley and Conover 1956; Peterson 1986; Capriulo et al. 2002). This pattern has not changed since the 1950s, and appears to be independent of location in the Sound (Figs. 11 and 12).

The long-term patterns from the CT DEEP monitoring program show a dramatic decrease of chlorophyll throughout the decade of the 1990s, a subsequent increase that happened throughout LIS, and a decrease in DIN, particularly in the West Narrows. From 1991-2005, significant decreases in annual mean and maximum DIN concentrations in surface waters were observed in the West Narrows. Mean DIN dropped from about 0.4 to less than 0.2 mg L^{-1} (slope

= -0.01 mg $L^{-1}y^{-1}$, $r^2 = 0.24$, $p = 0.084$, see caption in **Fig.** 11). Similar decreasing trends were observed for TDN and TN in that region for the same period (Dam et al. 2010). In contrast, there was no hint of a trend for DIN in the East Basin for the same period. The decreasing trend in DIN in the West Narrows is probably linked to the decrease in nutrient loading that has resulted from sewage-treatment improvements in that region.

The time-dependent pattern in chlorophyll concentration was different from the one for DIN. A dramatic decrease in chlorophyll was observed throughout LIS for the period 1988-1999, and no spring blooms were apparent during the years 1999 and 2000. Since 2000, chlorophyll increased and remained fairly constant with time. While there is a spatial correlation between nutrients and chlorophyll biomass, the two variables appear less correlated in time. That is, from 1988-2007 there was a system-wide change in chlorophyll with time, but not in DIN. The chlorophyll pattern perhaps reflects some regional forcing, whereas the DIN patterns appear to reflect the differential nutrient loading from east to west.

It is obvious from Figs. 11 and 12 that there is considerable interannual variability of phytoplankton biomass in LIS. However, there is no clear evidence of any trend in biomass from the early studies of the 1950s until the 2000s. The only fair comparison is the Central Basin since that is the region that was originally studied by G. Riley and coworkers. Figure 13 shows the chlorophyll concentration in the Central Basin for the period 1988-2005. The range of observations for this period is similar to 1952-1954, (Riley and Conover 1956; Conover 1956) and 1992-1995 (Capriulo et al. 2022). Furthermore, a comparison of decadal means in the different seasons of the year among the 1950s, 1990s and 2000s does not show any clear trends (Dam et al. 2010).

6.4.1.2 Phytoplankton Community Structure

Conover (1956) first reported that diatoms dominate the phytoplankton in LIS, except perhaps in summer when dinoflagellates and other small flagellates prevail. Capriulo et al. (2002) made the same observation, but noticed that peak abundance was not in spring, but summer and fall (see their **Fig.** 28). Since the early 2000s, Senjie Lin and coworkers have analyzed data from the CT DEEP phytoplankton monitoring program. They did microscopic identifications for 10 representative stations in 2002, 2003, and 2007-2010, and molecular analysis for the <5 µm size-fraction at four of the stations in 2003. Here, we summarize their findings. Although phytoplankton species number fluctuated somewhat interannually, the community structure was relatively stable, both in time and space (**Fig.** 14). Diatoms contributed 61% of the species richness and dinoflagellates accounted for 26%. Minor components included chrysophytes (2.6%), raphidophytes (2.1%), chlorophytes (3.1%), cryptophytes (1.0%), euglenophytes (0.5%) and a number of unidentified species (3.65%). Total species number exhibited two small peaks yearly, one in early spring and the other in late autumn, mainly attributable to diatom species (**Fig.** 14a). There was no discernable spatial trend in species richness along the Sound (**Fig.** 14b). These patterns resemble the observations from the early 1950s (Riley and Conover 1956; Harris and Riley 1956). A closer look at the 2002-2010 data showed that *Skeletonema costatum* was dominant in eastern LIS, *Skeletonema costatum* and *Thalassiosira* sp. in central LIS, and *Thalassiosira* sp., *Dactyliosolen fragilissimus* and *Thalassiosira nordenskioldii* in western LIS. Such spatial species differentiation could be a result of responses to eutrophication (Cloern 2001). But as diatoms were the unassailably predominant group in the phytoplankton community (Conover 1956; Harris and Riley 1956; Capriulo et al. 2002; Liu and Lin 2008), apparently the effect of eutrophication in LIS main water body is relatively low. However, it is well recognized that some inner bays have suffered severe eutrophication, where dinoflagellates such as *Prorocentrum minimum*, *Akashiwo sanguinea* and *Alexandrium fundyense*, can form blooms seasonally. For example, *A. fundyense* has formed blooms in Huntington Bay, New York, causing Paralytic Shellfish Poisoning outbreaks since 2006 (Hattenrath et al. 2010).

Although diatoms dominated the phytoplankton community throughout the year, seasonal variation in dominant species occurs. For 2002-2010, *Leptocylindrus minius*, *Scenedesmus* sp., *Thalassiosira* spp. and *Skeletonema costatum* were dominant in spring, *Thalassiosira* sp., *Dactyliosolen fragilissimus*, *P. triestinum*, *T. nordenskioldii* and *T. gravid* in summer; *S. costatum* and *Thalassiosira* sp. in fall, and *Thalassiosira* sp. and *Asterionellopsis glacialis* in winter. Historically, *S. costatum* was the predominant species in winter, while in summer, stratification and low inorganic nitrogen favored other species, especially dinoflagellates, of which *Gonyaulax* spp. could make up ~50% of the phytoplankton cell population (Harris and Riley 1956). In the last decade, a peak of dinoflagellate species number was noticeable in summer (**Fig.** 15a). *P. triestinum*, *P. minimum* and *P. micans* appeared to replace *Gonyaulax* spp. as dominant dinoflagellate species in western LIS in summer. Overall, *Thalassiosira* spp. and *S. costatum* were the predominant species in all seasons and almost the whole Sound. Recent molecular analyses have revealed several species out of the originally established *S. costatum* species; whether the observed S. costatum is composed of multiple species remains to be determined.

Very small phytoplankton, such as the ubiquitous cyanobacteria *Synechococcus* spp., have not been systematically studied in LIS, but they are known to be abundant, especially in summer. For example, Campbell (1985) measured abundances up to 1.8×10^8 cells L^{-1} in central

LIS (Crane Neck shore station). At 1-2 fg chl cell^{-1} (Liu et al. 1999), this equates to 0.18 to 0.36 μg chl L^{-1}, most likely less than 10% of the total phytoplankton biomass. Their role in primary production in LIS is not known.

6.4.1.3 Phytoplankton Abundance

Phytoplankton abundance in LIS varies seasonally, typically with a major peak in late winter or early spring, and a lower peak in the fall (Conover 1956; Harris and Riley 1956; Sun et al. 1994). During 2002-2010, the largest peak was apparent in the summer (**Fig.** 15a), which is in stark contrast to the work from the 1950s (Conover 1956), but similar to what was observed in the early 1990s in central LIS (Capriulo et al. 2002). The latter authors observed, however, the largest peak in phytoplankton abundance in the fall in western LIS. For 2002-2010, total abundance could reach about 4.4x10^{5} cells L^{-1} (2009) to 1.5x10^{6} cells L^{-1} (2007), of which diatoms contributed over half of the total biomass (~64%), while dinoflagellate accounted for about 11% (**Fig.** 15a). These figures are similar to those reported by Capriulo et al. (2002). Conover (1956) reported peaks in phytoplankton abundance that were an order of magnitude higher (up to ~ 30 million cells L^{-1}), but most of the observations fell within the range reported here.

As previously observed (Bowman 1977; Aller and Benninger 1981; Wolfe et al. 1991; Capriulo et al. 2002; Liu and Lin 2008), phytoplankton abundance was highest in the high nutrient and low salinity waters of the western Sound (**Fig.** 15b). As with the case for chlorophyll, most of the significant spatial differences in phytoplankton abundance arise from the extreme ends of LIS.

6.4.1.4 Primary Production

The few available measurements and estimates of primary production for LIS bracket the production between 400 and 854 g C m^{-2} y^{-1}. This two-fold range is not surprising given that different methods were employed in the studies, that sampling occurred in different regions, and that studies were done in three different decades. Riley (1956) provided a single estimate of annual gross primary production from the dark and light bottle technique. This estimate is 470 g C m^{-2} y^{-1}. That study cites work by Riley (1941) putting production at 600-1000 mg C m^{-2} y^{-1}. The estimate of production from Dam Guerrero (1989) is from short incubations during mid-day using the ^{14}C technique, which yields something between gross and net production. Measurements were integrated for the uppermost 10 m of the water column, and sampling frequency was weekly or biweekly from February to August. Sampling took place at a single station, near H6 (see **Fig.** 10), in central LIS. That study estimated primary production at 854 mg C m^{-2} y^{-1}, with virtually identical estimates for the winter-spring and the summer periods. Goebel et al. (2006) derived gross primary production from physiological parameters measured in oxygen-based photosynthesis-irradiance (P-I) incubations, integrated both through time of day and depth (uppermost 10 m). Sampling was biweekly during summer months and monthly during spring and fall. Eight stations from the central to western LIS were sampled. That study put net primary production at 400 ±80 mg C m^{-2} y^{-1}. Because algal respiration was assumed to be 50% of gross production in that study, the average gross production was 800 mg C m^{-2} y^{-1}. Thus, the estimates from Dam Guerrero (1989) and Goebel et al. (2006) are rather close.

The only study that has examined spatial variability in productivity in LIS is Goebel et al. (2006). They observed a gradient of declining productivity from west to east, which correlates with a similar gradient in nitrogen loadings and chlorophyll biomass. However, productivity only varies by a factor of two whereas nitrogen loadings vary by roughly an order of magnitude, while biomass varies by 3 to 5-fold. This implies that other factors must also constrain productivity. Indeed, nutrient addition assays indicate that nutrient limitation of primary production, either by N or Si, occurs in LIS (Gobler et al. 2006), but that this limitation varies with season and region. For example, western LIS appears N-limited during late spring and summer whereas such limitation occurs in central LIS from spring until fall. Grazing, which is discussed later, is another potentially controlling factor. The magnitude of the gradient in mesozooplankton abundance (see next section) from east to west matches that of chlorophyll and primary production. Provided that individual grazing rates do not decrease from east to west, then zooplankton grazing should have an effect on the chlorophyll and primary production.

6.4.2 Zooplankton

The first survey of zooplankton abundance and seasonality in LIS was done in the early 1950s (Deevey 1956), and was entirely restricted to metazooplankton. (The term mesozooplankton applies to organisms > 200 µm, and usually also refers to metazooplankton. The term microzooplankton applies to organisms < 200 µm, and usually refers to protozooplankton. For example, most copepod nauplii and some copepodid stages are small enough to be microzooplankton, but are also metazooplankton. Here, we use the term meta- and mesozooplankton interchangeably, as well as micro- and protozooplankton.). The first protozooplankton (unicellular heterotrophs) survey was done in 1979-1980 (Capriulo and Carpenter 1983). Both of these surveys were mostly confined to central LIS. Work on copepod phenology, also in the central Sound, resumed in the 1980s (Peterson 1986). The first temporal-spatial survey for both metazooplankton and protozooplankton was carried in the 1990s

(Capriulo et al. 2002), but was confined to three locations along the east-west axis of LIS (Capriulo et al. 2002). Since the early 2000s, a more comprehensive temporal-spatial survey of the zooplankton has been carried out by the CT DEEP monitoring program (Dam and McManus 2009). This program samples six stations along the east-west axis of the Sound. Here, we restrict comparisons among studies to central LIS, where sampling locations are common to all studies. With respect to the metazooplankton, Deevey (1956) sampled monthly with a No. 10 silk net (~ 158 µm mesh) near the LISS/CTDEEP station H4 in the Central Basin from March 1952 to May 1953. Sampling was from bottom to surface waters, although it is unclear if the tows were oblique or vertical. Capriulo et al. (2002) sampled monthly from 1993 through 1995 (landward of station H2). Oblique tows from bottom to surface were done with a 202 µm mesh. Dam and McManus (2009) data is from the CT DEEP zooplankton monitoring program. Sampling was monthly, or bimonthly during the summer months, and consisted of vertical tows from bottom to surface with a 202 µm mesh net. Peterson (1986) sampled approximately weekly from February to November in the early to mid 1980s (near station H6). Tows were vertical from bottom to surface with a 202 µm mesh net. However, we do not include Peterson’s data in all the comparisons because sampling did not take place throughout the entire year. Protozooplankton samples were collected from whole water samples, preserved and concentrated after settling, and then counted under inverted microscopes (Capriulo and Carpenter 1983; Capriulo et al. 2002; Dam and McManus 2009).

6.4.2.1 Metazooplankton

The seasonal cycle of metazooplankton abundance for the early 1950s (Deevey 1956) and the 2000s (Dam and McManus 2009) is shown in **Table** 2. The minimum abundance occurs in

January and the maximum in June, regardless of the year, and abundance varies by one order of magnitude throughout the season. The seasonal pattern of total mesozooplankton biomass for 2002-2009 (Dam and McManus 2009) is similar, but with peaks between April and May (**Fig.** 16). The offset in peak abundance and biomass is likely due to the biomass dominance of the copepod *Temora longicornis* relative to the *Acartia* species (**Fig.** 16). *T. longicornis,* a larger species than *Acartia*, peaked in May during this time period.

Copepods account for 80-90% of the metazooplankton abundance in LIS (Dam and McManus 2009). The following taxa have been routinely reported for LIS: Arthropoda (copepods, mysids, crab larvae, amphipods, barnacle nauplii and cladocerans); Annelida (polychaete larvae); Mollusca (gastropod and bivalve larvae); Echinodermata (sea star larvae); Chordata: *Oikopleura* sp.; Bryozoa; and Chaetognatha *(Sagitta elegans).*

The seasonal cycle of zooplankton species in LIS is characterized by two distinct assemblages (Peterson 1986). The winter-spring assemblage is dominated by the copepods *Acartia hudsonica* (abundance) and *Temora longicornis* (biomass). *Pseudocalanus* sp. is also present at this time, but in much lower abundance relative to the other two species. The summer-fall assemblage is dominated by the copepod *Acartia tonsa*. Two other species, *Paracalanus crassirostris* and *Oithona similis* are also abundant during this time period. Copepod species abundance data were examined for the 1950s (Deevey 1956), 1980s (Peterson 1986 and unpublished observations), 1990s (Capriulo et al. 2002) and 2000s (Dam and McManus 2009). *A. tonsa* peaked in late August 1952 at ~ 80,000 individuals m^{-3}. From 1982-1987, maximum *Acartia tonsa* abundance also occurred in August, but the peaks ranged from 2,000 to 25,000 individuals m^{-3} (Peterson 1986 and unpublished data). Similarly, from 1993-1995, *A. tonsa* peaks ranged from 3000 to 25,000 individuals m^{-3} (Capriulo et al. 2002). The peak *A. tonsa* abundance from 2002-2009 ranged from 15,000 to 160,000 individuals m^{-3}, with peak abundance usually in August (**Fig.** 16). Estimates for *A. hudsonica* abundance during the March peak were 70,000 individuals m^{-3} in the 1950s, 15,000 individuals m^{-3} in the 1980s, 30,000 individuals m^{-3} in the 1990s. During the 2000s, peak abundance ranged from 15,000 (March 2002-2003) to 300,000 m^{-3} (June 2003, **Fig.** 16). *T. longicornis* abundance peaked in June, with 60,000 individuals m^{-3} in the 1950s, a range from 10,000 to 45,000 individuals m^{-3} in the 1980s, a mean of 40,000 individuals m^{-3} in the 1990s. During the 2000s, peak abundance was in May or June and ranged from 25,000 to 141,000 individuals m^{-3} (**Fig.** 16).

The seasonal patterns of abundance and the species composition of the zooplankton appear relatively unchanged since the 1950s, with the exception of a very recent change in the phenology of *Acartia tonsa.* Typically this species is found in LIS from June to December. However, during 2008- 2009 (Dam and McManus 2009) and in 2010 (unpublished observations), *A. tonsa* in western LIS was present from June until April. If this change persists, then we might be witnessing a broadening of the growth season of this species.

There are clear decadal differences in zooplankton abundance (**Fig.** 17). Mean annual zooplankton abundance during 2002-2004 was lower than1952-53. Notice that most of the observations for 2002-2004 fall below the 1:1 line in **Fig.** 17. This is not the case for the comparison of 1952-53 to 2008-2009. There was no difference in mean annual zooplankton abundance between these latter two periods.

Zooplankton abundance from the 2000s (Dam and McManus 2009) was generally higher than what was reported for the early 1990s by Capriulo et al. (2002). This could be due to the locations of the stations in the latter study, which were in relatively shallow water. Also, the means reported in that study are geometric and the ones in the former are arithmetic.

Alternatively, this difference reflects the kind of decadal variability shown in **Fig.** 17. The lower zooplankton abundance during the 1990s could be explained by the dramatic decrease in phytoplankton biomass during that period.

Capriulo et al. (2002) examined zooplankton spatial distribution during the 1990s. They sampled three stations in relatively shallow water (about 10 m deep) between Stamford (western end) and Madison (eastern end), on the north side of LIS. Here, we highlight the data collected by the CT DEEP zooplankton monitoring program (Dam and McManus 2009), which has greater spatial (six stations from end to end in the Sound) and temporal (most of the last ten years) coverage. The mean yearly total metazooplankton abundances show a monotonic pattern of decrease from west to east that is consistent from year to year, with differences of 3 to 5-fold between the extreme ends of the Sound (**Table** 3). However, the annual variability within stations is such that that the only consistent statistically significant difference occurs between stations B3 and K2, the extreme ends of the Sound. This pattern, although not the details, is consistent with Capriulo et al. (2002) who also observed a decreasing gradient of zooplankton concentration from west to east. However, in that study the range of abundance varied by a factor of three, not five. The stations in that study, however, were not as far apart. In any case, the decreasing trend of zooplankton abundance from west to east mirrors the gradient in phytoplankton biomass (Figs. 11 and 12) and abundance (**Fig.** 14), and may suggest that metazooplankton are generally food-limited in LIS. There is no indication that the high degree of eutrophication in western LIS is negatively affecting the zooplankton community, at least in terms of abundance.

6.4.2.2 Protozooplankton

The most common protozooplankton in the ocean are heterotrophic nanoflagellates, ciliates and heterotrophic dinoflagellates. Currently, there is information on seasonal and spatial patterns of the first two groups in LIS. The first study of the seasonal cycle of protozooplankton in LIS was on ciliates, and reported abundances of ~270-2000 L^{-1} for most of the year, with peak abundance of $1.3x10^4$ L^{-1} in summer, in central LIS (Capriulo and Carpenter 1983). Tintinnids overwhelmingly dominated the ciliate community, with the exception of late spring (op. cit). At the time, 28 species of ciliates were reported. The list of ciliate species increased to 71 in the subsequent study of the early 1990s (Capriulo et al. 2002). Species richness decreased from west to east, with 94% of the reported species found in western LIS and 62% in eastern LIS. However, no information on abundance and seasonal cycles of ciliates was reported in that study.

In the CT DEEP monitoring program, ciliates are reported as three separate categories: tintinnids, other (naked) heterotrophic ciliates, and *Mesodinium rubrum* (now known as *Myrionecta rubra*). The latter is a mixotrophic ciliate (i.e. it eats phytoplankton but also photosynthesizes), but its main trophic mode is autotrophy, so it is effectively a phytoplankter. Examples of annual cycles of abundances of tintinnids, naked ciliates, and *M. rubrum* are shown in **Fig.** 18. A summary of abundance for 2002-2009 is shown in **Table** 4. All three groups show broad peaks in abundance from spring through summer, but with great spatial and temporal variability (**Fig.** 18). Tintinnids in particular can vary by orders of magnitude from one station to the next and from one survey to the next. Naked or aloricate ciliates, which were comprised chiefly of oligotrichs (e.g. *Strombidium* spp.) and non-tintinnid choreotrichs (e.g. *Strobilidium* and *Strombidinopsis* spp.), were usually more abundant than the lorica-bearing tintinnids. Although not shown here, small aloricate forms (10-15 µm), which are probably bacterivorous

(Sherr et al. 1986), were sometimes abundant, especially in western LIS. These ciliates contribute relatively little biomass to the microzooplankton assemblage because of their small size (e.g. at their most abundant, ciliates less than 20 µm in diameter were about 2/3 of the total ciliate abundance, but only 2.3% of the total biomass).

Both tintinnids and naked ciliates show a gradient from high abundance in western LIS to lower abundance in the east (**Fig.** 19). Most of this is driven by high abundance at station B3, westernmost Sound, and low abundance at K2 (easternmost Sound), which also showed the highest contrast in the metazooplankton. As in the case of the metazooplankton, statistically significant differences among stations were only apparent between stations B3 and K2. *Myrionecta*-like autotrophic ciliates did not show a predictable pattern among stations.

Maximum ciliate abundance for 2002-2009 for LIS (**Table** 4) is similar to the earlier report by Capriulo and Carpenter (1983); however, mean abundance appears relatively low. This is probably because the former values include the easternmost stations, which typically have the lowest abundances.

McManus (1986) reported abundances of heterotrophic nanoflagellates that ranged from about 200 to 8000 cells mL^{-1}, with a broad peak occurring during the summer in central LIS. Similar abundances were reported by Capriulo et al. (2002). Over their three-year study, average abundance ranged between 10^2 and 6.4×10^3 mL^{-1}, which is two orders of magnitude greater than the ciliate abundance. The authors reported significantly higher concentrations in the westernmost waters relative to central and eastern LIS. Peak abundance was during the summer, and there was considerable interannual variability in abundance. Beyond those two studies, there have been few measurements of these organisms in LIS. As bacterivores, they are a component of the microbial food web, which cycles inorganic nutrients and mineralizes organic carbon (Taylor 1982).

6.4.3 Fate of Primary Production

The main loss terms of net productivity are grazing, sinking and advection. However, there have been no concerted studies that attempt a budget of the primary production and its loss terms at different times of the year, or in different regions of LIS. Here we highlight what is known about the main loss terms for the production.

6.4.3.1 Grazing

Microzooplankton often account for a significant fraction of phytoplankton mortality, particularly in warmer months, in most aquatic environments (Calbet and Landry 2004, but see Caron et al. 2000). An early study conducted using seawater from the central basin of LIS and size-fractionated for grazing experiments (i.e., < 35 µm for prey and > 35 to < 202 µm for predator additions) found that microzooplankton, which in those samples consisted primarily of tintinnids, grazed ~ 12 % d^{-1} of the standing stock of phytoplankton in November and between 14 - 41 % d^{-1} in June (Capriulo and Carpenter 1980). Although summer ambient seawater temperatures were warmer, in the laboratory temperature had no discernible influence on individual clearance rate (Capriulo 1982). Grazing percentage (P), however, is determined by both the abundance of grazers and individual feeding rate, and microzooplankton abundances were substantially higher in June than in November (6,700 – 10, 500 organisms L^{-1} versus 1,900 – 2,500 L^{-1}, Capriulo and Carpenter 1980).

In a recent study in western LIS, York et al. (2011) measured microzooplankton grazing rates during March and between June and July over two years using the dilution technique (Landry and Hassett 1982). Significant grazing (g d^{-1}), as measured by changes in total chlorophyll *a*, was detected 50 % of the time in winter (mean g ± s.e. = 0.24 d^{-1} ± 0.12, n = 9) and 62.5 % in the summer (0.66 d^{-1} ± 0.19, n = 16). (The authors suggested that at those times when grazing was not detected, suspended, non-food particles may have interfered with the efficient removal of phytoplankton cells by the micrograzers). Grazing coefficients (i.e., g) can be used to estimate the grazing impact of microzooplankton on phytoplankton standing stock (% removed d^{-1}, as above), where $P = (1 – e^{-g}) \times 100$ (after Verity et al. 2002). Using this approach, the mean grazing impact (± s.e.) for western LIS based on the data of York et al. (2011) was 17.5 % d^{-1} ± 8.1 and 37.2 % d^{-1} ± 8.2 for March and June-July, respectively. Although the dilution technique is a different methodological approach, these estimates of P are remarkably similar to those of Capriulo and Carpenter (1980) for both the cold and warm temperature periods. Furthermore, the seasonal shift in P in western LIS corresponded to change in microzooplankton biomass (mean ± s.e; March = 6.6 ± 1.1 µg C L^{-1}, and June-July = 30.4 ± 1.1 µg C L^{-1}; York et al. 2011), and represented a similar summer population increase (~ 4X) as previously noted in central LIS. As compared to metazooplankton (e.g., copepodites and adult copepods), micrograzers may be more efficient at consuming smaller phytoplankton cells and less able to consume larger items, such as chain-forming diatoms that often dominate during the spring bloom in LIS. For example, maximum prey sizes of 10 µm and 55 µm cell diameter were noted for two species of heterotrophic dinoflagellates (Hansen and Calado 1999 and references therein). Grazing coefficients trended higher on smaller phytoplankton cells as determined from changes in < 10-µm chlorophyll *a* (mean g ± s.e = 0.85 d^{-1} ± 0.21: York et al. 2011) compared to total chlorophyll *a* in the dilution experiments, though the results were not statistically significant.

Less is known about the grazing impact of the total metazooplankton community on phytoplankton in LIS, and studies conducted to date have focused on a particular copepod species, albeit at times a dominant species such as *Temora longicornis* during late winter and spring (Dam and Peterson 1991; Capriulo et al. 2002). A study of the *in situ* feeding of female *T. longicornis* suggested that this population alone could remove between < 1 % and 34 % d^{-1} of the phytoplankton standing stock in the central basin (Dam and Peterson 1993). The highest impacts tended to be found between mid- to late spring (~ 10 – 34 % d^{-1}) while lower values were in late winter and mid-summer (< 1 – 2 % d^{-1}). Dam Guerrero (1989) estimated an average removal of 20% of the primary production by *T. longicornis*. The grazing impacts were not significantly related to the population abundance of the copepods (**Table** 6 in Dam and Peterson 1993), but instead, likely due to confounding environmental influences on copepod feeding behavior. The grazing impact of a population is determined by both population abundance and individual ingestion rate. Individual ingestion rate of copepods (e.g., ng chlorophyll *a* $individual^{-1}$ h^{-1}) is often measured as a function of gut-pigment content and gut-clearance rate (Båmstedt et al. 2000). For *T. longicornis* females, several factors influenced individual gut-pigment content including phytoplankton size-structure and abundance (Dam and Peterson 1991, 1993). The gut-pigment content of *T. longicornis* females was highest during the spring bloom when the phytoplankton community was dominated by larger cells (> 20 µm) and lowest in late spring and early summer when phytoplankton abundance was lower. The gut-clearance rate of these copepods was also positively related to seawater temperature (Dam and Peterson 1988).

The grazing impact of *Temora longicornis* during spring in LIS may be on par or even higher than microzooplankton grazing. The situation in summer and fall is likely to be different. The calanoid copepod *Acartia tonsa* is a dominant member of the zooplankton community during summer and fall (Capriulo et al. 2002), and is typically an omnivore with a partial dietary dependence on heterotrophic prey, such as ciliates, to fuel reproduction (Gifford and Dagg 1991). Dam et al. (1994) found that phytoplankton (i.e., chlorophyll *a*) ingestion rate and egg production rate (eggs female^{-1} d^{-1}) of *A. tonsa* were better correlated to the > 10-µm size-fraction compared to total chlorophyll *a*, and that maximum ingestion rates (Figure 1 in Dam et al. 1994) occurred during the fall bloom in September. Using *in situ* abundance estimates and ingestion rates, Dam Guerrero (1989) estimated that *A. tonsa* removed on average 4% of the primary production. In another Long Island estuary, Great South Bay, mesozooplankton dominated by *A. tonsa* in summer, consumed 1 – 4 % d^{-1} of total primary production in summer (Lonsdale et al. 1996). These results indicate a substantial difference in the trophic role of these two copepod species in LIS. Whereas *T. longicornis* may play a substantial role in the control of phytoplankton in spring, the same is less probable for *A. tonsa* during summer and fall. Although carnivorous feeding behavior has not been investigated in LIS *per se*, it likely contributes to the reproductive success of both *T. longicornis* and *A. tonsa* (Gifford and Dagg 1991; Dam et al. 1994; Peterson and Dam 1996; Lonsdale al. 1996).

Because the abundance and biomass of zooplankton is heavily dominated by *Temora longicornis* and the two *Acartia* species, grazing estimates of these species are probably good proxies for total mesozooplankton grazing. To date there is no single widely accepted technique to measure total mesozooplankton grazing akin to the dilution technique for microzooplankton grazing. Dam Guerrero (1989) used the downward flux of zooplankton fecal pellets captured by free-drifting sediment traps (Welschmeyer and Lorenzen 1985) to estimate mesozooplankton grazing impact during the spring season of 1987. He concluded that mesozooplankton removed ~ 25% of the total primary production during that season. Total mesozooplankton grazing and *Temora longicornis* grazing for the same period were significantly and positively correlated (r = 0.58), and grazing by *T. longicornis* accounted for 80% of the total mesozooplankton grazing. No similar exercise has been carried out for the summer-fall period. Riley (1956) estimated, based on calculations of carbon required to satisfy metabolic demands of copepods, that zooplankton consumed 26% of the annual primary production.

In summary, all indications are that during the winter and spring micro and mesozooplankton each remove about 25% of the primary production, for a total of 50%. During the summer and fall, microzooplankton grazing is more than 50% of the primary production and mesozooplankton grazing is much less. During the LISICOS study in the Narrows regions of the Sound (westernmost end of LIS) in July 1995, microzooplankton grazing was estimated to remove up to 75% of the primary production (York et al. 2011) whereas mesozooplankton removed < 20% of the production (H. Dam, unpublished).

6.4.3.2 Sinking and Horizontal export

Phytoplankton sinking from the water column to the benthos and horizontal export via advection can be significant loss terms for primary production. However, both of these terms are poorly constrained for LIS. For example, during the spring season of 1987, phytoplankton sinking flux as measured by free-drifting sediment traps, was estimated to be 2.6-fold greater than mesozooplankton grazing (Dam Guerrero 1989). Since mesozooplankton grazing was estimated at the time to be 25% of the primary production, by this accounting, loss due to sinking was the equivalent of 65% of the primary production. Because all other loss terms (microzooplankton grazing, horizontal export) would only account for the remaining 10%, the sinking loss term was probably overestimated. During the 1995 LISICOS study of the Narrows region of the Sound, phytoplankton sinking flux was measured with both moored and free-drifting sediment traps, and estimated to account for 3-30% of the primary production. By difference from grazing (see above) and sinking, losses due to horizontal export had to be < 20%. Strikingly, community respiration exceeded primary production by about an order of magnitude (J. Kremer, personal communication). Therefore, a mass balance could not be achieved. A similar exercise has not yet been attempted for the spring season, where a significant fraction of the annual production takes place. In any case, the unbalanced carbon budget from the LISICOS studies suggests that portions of the Sound might be highly heterotrophic. This implies that a large source of terrestrial or oceanic, not estuarine, carbon must exist to sustain the respiratory demands in the water column. In summary, there is a great deal of uncertainty as to the role of sinking and horizontal export of the primary production. Integrated studies in which primary production and its loss terms are simultaneously measured are required.

6.4.4 Harmful Algal Blooms

Harmful algal blooms (HABs) occur when a single species of phytoplankton grows to a density that has a direct negative impact upon other organisms or an ecosystem through production of toxins, mechanical damage, or by other means. HABs often are associated with shellfish-poisoning syndromes in human consumers of contaminated molluscs, economic losses to coastal communities and commercial fisheries, and HAB-associated invertebrate, fish, bird, and mammal mortalities. These events are sometimes referred to as ‘red tides’ because the microalgae that most frequently cause HABs, dinoflagellates, often contains a reddish pigment (peridinin), and thus can discolor waters red when blooms occur. Some dinoflagellate blooms that color waters red are harmless and, because blooms caused by other groups of algae with different coloration (green and brown) also can be harmful, the term “harmful algal blooms,” or HABs has been adopted by scientists to describe these diverse events. All algal blooms are not harmful or toxic and many HABs do not impart any discoloration to the water.

Globally, the phytoplankton communities within many coastal ecosystems have undergone phase shifts in recent decades, with species associated with HABs becoming more prevalent (Hallegraeff 1993; Glibert et al. 2005; Heisler et al. 2008). The number of species, duration, intensity, and distribution of HABs all have increased, accelerating negative impacts on human health, fisheries, and economies. Some parts of LIS are prime examples of regions undergoing such changes with regard to HABs. Prior to 2006, algal blooms in LIS were viewed as nuisances and contributors to hypoxia. Since that time, toxic and harmful algal blooms have occurred annually within some parts of the estuary. For example, since 2006, blooms of the saxitoxin-producing dinoflagellate *Alexandrium fundyense* have emerged in Northport and Huntington Bays along the north shore of Long Island every spring. These blooms persist for ~ two months (late April through June), and achieve cell densities $>10^6$ cells L^{-1} and water-column saxitoxin concentrations $>2.4 \times 10^4$ pmol STX eq. L^{-1} (Hattenrath et al 2010). During the blooms, shellfish have become highly toxic to humans (>1.4 mg STX eq. $100g^{-1}$ shellfish tissue) resulting in the closure of nearly 10,000 acres of shellfish beds in Northport and Huntington Bays during five of the past six years since 2006 (**Fig.** 20; Hattenrath et al. 2010).

Hattenrath et al. (2010) investigated factors promoting *A. fundyense* blooms in Northport Bay. Densities of benthic *A. fundyense* cysts at the onset of blooms generally have been orders of magnitude lower than levels needed to account for observed cell densities, indicating that *in situ* growth of vegetative cells is responsible for peak bloom densities. Experimental enrichment of bloom water with biologically available nitrogen, particularly ammonium, significantly increased densities of *A. fundyense* and saxitoxin concentrations relative to unamended control treatments (Hattenrath et al 2010). The □^{15}N signatures (12 to 23‰) of particulate organic matter (POM) during blooms were similar to those of sewage (10 to 30‰), and both toxin and densities of *A. fundyense* were significantly correlated with POM □^{15}N ($p < 0.001$; Hattenrath et al 2010). These findings suggest that *A. fundyense* growth was supported by a source of wastewater, such as the sewage treatment plant which discharges into Northport Harbor. Warmer than average atmospheric temperatures in the late winter and spring of 2008 and a cooler May contributed to an extended period of water column temperatures optimal for growth of *A. fundyense* (12 – 20ºC), and thus may have contributed to the larger and longer bloom in 2008 (Hattenrath et al. 2010). Altogether, this evidence suggests that sewage-derived N loading coupled with above-average spring temperatures can promote intense and toxic *A. fundyense* blooms in embayments within LIS. The persistence of a dense cyst bed (>500 cysts cm^{-3}) in Northport Harbor sediment since the onset of these blooms is likely responsible for the persistent nature of these events, but perhaps not their interannual intensity.

Blooms of *A. fundyense* recently have been most intense in Northport and Huntington Bays, but surveys of LIS from 2008 – 2011 have demonstrated that undetected blooms of *A. fundyense* had occurred in multiple near-shore regions of NY and CT, with low abundances of these species present even within open water regions of LIS. For example, in 2009, a bloom of *A. fundyense* in LIS near the Mattituck Inlet was denser than the blooms in Northport and Huntington Bays. Moreover, elevated levels of *A. fundyense* now have been confirmed at more than 25 sites across NY and CT, demonstrating that these HABs are not an isolated phenomenon in a single harbor. The widespread distribution of *A. fundyense* highlights the potential for this toxic dinoflagellate species to expand across LIS if the suitable conditions such as those currently present in Northport (cyst beds, high nitrogen loads, poor flushing) are replicated elsewhere.

The dinoflagellate *A. fundyense* is not the only species of toxic phytoplankton that blooms in LIS. In 2008, another dinoflagellate, *Dinophysis acuminata*, began forming large and persistent annual blooms (>10^6 cells L^{-1}) in Northport Bay. These blooms have recurred annually since then, and the species forming these blooms has been confirmed as *Dinophysis acuminata* by scanning electron microscopy. This species has been responsible for diarrhetic shellfish poisoning (DSP) events around the world (Yasumoto et al. 1980; Hallegraeff and Lucas 1988; Campbell et al. 2010), and the blooms in 2008 and 2010 generated the toxins okadaic acid and DTX-1 (Steve Morton, NOAA, pers. comm.), both of which are the causative agents of DSP-syndrome and are federally regulated by the US Food and Drug Administration. Blooms of *Dinophysis* have been reported on the east coast of the U.S. (Maranda and Shimizu 1987; Tango et al. 2004), although DSP-causing toxins in shellfish had not been reported above the action level in the US until recently. Campbell et al. (2010) reported that in 2008, a bloom of *Dinophysis* exceeding 10^5 cells L^{-1} occurred in the Gulf of Mexico causing DSP-toxicity in oysters and the closure of shellfish beds. Although the co-occurrence of *Dinophysis* blooms and other dinoflagellates in LIS suggests that they are promoted by similar factors, there have been few field studies investigating factors that promote *Dinophysis* blooms. Currently, the factors promoting blooms of *D. acuminata* in LIS are unknown. Moreover, the occurrence of DSP in

LIS represents a serious development, as the NYSDEC is not currently monitoring for *D. acuminata* or DSP toxins in the water column or shellfish.

Another dinoflagellate species with harmful and ecosystem-disruption effects that blooms episodically in LIS is *Prorocentrum minimum*. This species has been reported in LIS as a spring-summer bloom-forming phytoplankter for as long as records have been published, although it may be listed under species pseudonyms *Exuviella minimum*, *Exuviella marie-lebouriae,* or *Prorocentrum marie-lebouriae* (Riley et al. 1956; Riley and Conover 1967; Capriulo et al. 2002). This species was recognized only recently as a “harmful” species (Heil et al. 2005). Possible associations with shellfish poisoning in human consumers have not been verified, and a toxin responsible for harmful effects upon shellfish and other invertebrates has not been characterized, leading some to speculate the bloom effects are attributable to excessively high biomass loading leading to hypoxia (Landsberg 2002).

Association of *P. minimum* blooms with poor performance of larval and post-set shellfish in the Milford Aquaculture Laboratory’s shellfish hatchery in the 1950s and 1960s were documented (Davis and Chanley 1956), leading to studies exploring the possibility that trichocysts released by the dinoflagellate cells were responsible for molluscan responses (Ukeles and Sweeney 1969). A particularly widespread (Throgs Neck to New Haven) and long-lived (May-August) bloom of *P. minimum* in 1987 was associated with massive fish kills and caused arrested growth and mortality in northern quahogs (*Mercenaria mercenaria*) planted near Stamford and Milford as part of a growth study being conducted by the Milford Lab (Wikfors and Smolowitz 1993). Subsequent experimental studies revealed that *P. minimum* varies greatly in “toxicity” to shellfish, with declining populations being more bioactive (Wikfors 2005; Li et al. in press). Most bivalve species are able to protect themselves against *P. minimum* exposure for at least a few days by rejecting captured cells in pseudofeces or through post-ingestive rejection within hemocyte-coated fecal strands (Hégaret et al. 2008). This dinoflagellate likely has episodic, negative effects upon farmed and wild populations of bivalves annually within LIS embayments, but there is no obvious trend in occurrence since the 1950s; therefore, this organism could be considered a stable component of the LIS plankton ecology.

The ichthyotoxic dinoflagellate *Cochlodinium polykrikoides* is a catenated, bloom-forming species that has become increasingly common in coastal zones around the world (Kudela and Gobler 2012). Historically, blooms of *C. polykrikoides* have been reported most frequently in Asia, with South Korea alone reporting more than $100 million USD in annual fisheries losses attributable to this species during the 1990s. Since 2004, this species has been forming dense blooms in the waters of eastern Long Island, including the Peconic Estuary that exchanges with eastern LIS (Gobler et al. 2008; Kudela and Gobler 2012). To the north of this region, blooms have been observed recently in Point Judith Pond, RI (Hargraves and Maranda 2002) as well as in Narragansett Bay (S.E.S, pers. obs.), Martha's Vineyard and Nantucket, MA (GHW pers. obs.), although scientific reports of the latter sites have yet to be published. This species has been known to be transported hundreds of km across the waters of Asia (e.g. Korean to Japan; Malaysia to the Philippines; Kudela and Gobler 2012). It seems likely that such transport has already occurred across eastern LIS. Furthermore, it seems plausible that such transport could introduce blooms into new, coastal regions of LIS in the future.

Similar to *Prorocentrum minimum*, the toxic diatom *Pseudo-nitzschia multiseries* appears to have been a component of the LIS phytoplankton for as long as records have been kept, but under the pseudonym *Nitzschia seriata* (Riley et al. 1956; Riley and Conover 1967). Several species in this genus produce domoic acid, a glutamic-acid analog that can be transferred through filter-feeding shellfish to human seafood consumers in whom it can cause Amnesic Shellfish Poisoning (ASP). *Pseudo-nitzschia* spp. generally are seen as components of the mid-to-late spring bloom, but seldom dominate the assemblage. Currently there are no reports of domoic-acid poisoning in humans or wildlife in LIS and no clear trends in extent or intensity of occurrence.

A final phytoplankton species that forms HABs near LIS is *Aureococcus anophagefferens*. *A. anophagefferens* is a pelagophyte that has been causing destructive brown tides in northeastern and mid-Atlantic U.S. estuaries for more than 25 years, with blooms occurring most frequently in Long Island waters. Large blooms (> 10^6 cells ml^{-1}) effectively shade the benthos causing reduction in eelgrass beds (Cosper et al. 1987). Brown tide caused recruitment failure and starvation in bay scallop populations (Bricelj et al. 1989) and high rates of mortality in bivalve molluscs during blooms (Bricelj et al. 2001; Greenfield and Lonsdale 2002) generally have been attributed to cessation of feeding and starvation (Gainey and Shumway 1991). Blooms have occurred consistently within Long Island south-shore estuaries since 1985, but occurred in the Peconic Estuary on eastern Long Island from 1985 through 1995 only (Gobler et al. 2005). Quantification of *A. anophagefferens* by the Suffolk County Department of Health Services in harbors along the NY coastline of LIS revealed the widespread presence of *A. anophagefferens* cells, with maximal densities of 5 x 10^3 cells ml^{-1}-- an order of magnitude lower than the levels known to inhibit shellfish feeding (Bricelj et al. 2001). Given the departure of blooms from the neighboring Peconic Estuary and the low levels of *A. anophagefferens* typically present in LIS, brown tides are one of the HABs less likely to occur in LIS in the near future.

At greatest risk of being impacted by a possible change in the HAB ecology of LIS is its $80-million molluscan shellfish fishery, chiefly consisting of wild-caught northern quahogs, and bottom-cultivated eastern oysters, *Crassostrea virginica*. Shellfish-harvest closures because of fecal-indicator bacteria are common in LIS, but until the recent *Alexandrium fundyense* blooms on the north shore of Long Island, the shellfish industry in LIS has been largely immune from the PSP closures that plague northern New England shellfisheries. The state resource agencies in New York and Connecticut responsible for assuring the safety of shellfish landings – Department of Environmental Conservation in New York and the Department of Agriculture in Connecticut – have monitoring and control programs approved by the US Food and Drug Administration to detect the presence of toxigenic algae in the water and/or toxins in shellfish tissues. These surveillance programs will need to keep pace with changing conditions in the phytoplankton ecology of LIS to maintain the economic benefits of a thriving shellfishery in LIS.

6.4.5 Science Gaps and Management Implications

There is remarkable agreement in the spatial patterns of abundance and biomass of phytoplankton, protozooplankton and metazooplankton in LIS; there is a decreasing gradient from west to east, but it is mostly underlain by differences at the extreme ends of the Sound. This gradient has some implications for the two major problems in LIS, eutrophication and hypoxia. Clearly, there is some degree of correlation between these two variables in the Sound. Western LIS, with its high nutrient concentration and high phytoplankton biomass, experiences summer-time hypoxia, whereas the eastern Sound does not (Lee and Lwiza, 2008; O’Donnell et al. 2008). However, the linkage is complex. Nutrient concentrations, specifically DIN, have been steadily declining in the western Sound (**Fig.** 11), and chlorophyll decreased by at least a factor of five during the 1990s (**Fig.** 11), yet summer-time hypoxia pervasively occurred in western LIS during this period (Lee and Lwiza 2008). Thus, further work is necessary to elucidate the mechanistic linkages between nutrients, phytoplankton biomass and hypoxia.

There is considerable interannual (e.g., chlorophyll, Figs. 11 and 12) and decadal (metazooplankton, **Fig.** 17) variability in the plankton in LIS. Such variability has implications for resource limitation of consumers; for example, the low zooplankton abundance during the early 1990s might have reflected the dramatic decrease that was taking place in chlorophyll at the time. Because the changes in chlorophyll and zooplankton took place throughout the Sound, this suggests some regional rather than local forcing. Finally, there is no clear evidence that LIS is now more eutrophic than 60 years ago, as both nutrient and chlorophyll levels do not seem to have changed much since then.

Capriulo et al. (2002) hypothesized that the high abundance of copepods in western LIS could be a factor in the development of hypoxia in that region due to the production of fecal pellets that would quickly sink to the bottom and decompose there. This hypothesis was tested recently. Fecal pellet production rates, zooplankton standing stocks, the downward flux of fecal pellets and the standing stock of fecal pellets in the water column were measured in LIS in July 2005 and March 2006 (Loglisci 2007). She estimated that pellet carbon flux was the equivalent of 2.3 – 45.2% of the total particulate organic carbon flux. Further, she estimated that if the entire sinking pellet pool degraded on the seafloor, it would account for up to 88% of the total sediment oxygen demand in March, but only 18% in July. Thus, while fecal pellets can represent a significant drawdown of DO during the winter, this is not a time when hypoxia is a problem. On the other hand, when hypoxia is prevalent, zooplankton pellets account for at best ~20% of the drawdown of DO.

Finally, in terms of developing management strategies for hypoxia in LIS, a significant gap in knowledge and understanding is the fate of the primary production. There are very large imbalances between sources and sinks of carbon in western LIS, where hypoxia is common. A concerted effort is required to address this gap in knowledge.

6.5 Deep Water Benthos

6.5.1 Deep Water Benthic Habitats and Macrofaunal Communities

The sea floor of LIS is primarily comprised of sedimentary environments that form physical habitat mosaics of varying spatial extent, scale and complexity (**Fig.** 21). These soft-sediment environments are dotted with patches of hard substrates such as boulder fields and rocky outcrops, adding to the overall diversity of sea floor habitats in LIS. Superimposed on the physical habitat structure are biogenic structures such as tubes, pits, burrows, shell hash and structures by habitat-forming species such as mussels and hydrozoans (**Fig.** 22). The relative mix of overall habitat structure and complexity varies across spatial scales and sediment patch type. The communities that are found in these habitats are typically dominated by polychaete annelids, various crustacean taxa such as amphipods, and bivalves and gastropods that are primarily infaunal or live on the sediment surface. This section focuses on the soft-sediment habitats and communities of the deeper reaches (> 3-4 m depth) of LIS, review our current state of knowledge of these communities, provide an assessment of what aspects of LIS benthos need to be better understood, and the types of studies that may provide the necessary information.

6.5.1.1 Studies prior to 1985

Prior to 1985, our knowledge of the benthic ecology of the deep-water portions of LIS was based on a handful of Sound-wide surveys and several sets of studies in specific portions of LIS (**Fig.** 23). Sanders (1956) and McCall (1975) studied the benthos of the central basin of LIS, revealing the general nature and composition of these communities, primarily those inhabiting mud and sandy-mud habitats. McCall (1977), Rhoads et al. (1978) and others (see Biogeochemistry chapter) conducted more detailed studies of the mud communities in the central basin in some detail, particularly with respect to animal sediment relations, how they affect sediment biogeochemistry, and their responses to disturbances and subsequent recovery / successional dynamics. Portions of this work were tied to the study of dredged material disposal sites by the Army Corps of Engineers (DAMOS project, see Benthic Disturbance section later in chapter). These studies led to a widely applied model of soft-sediment community recolonization and succession (**Fig.** 24), and also technological developments to study soft-sediment communities, specifically the development of the REMOTS camera for sediment profile imaging (see Rhoads and Germano 1982), and the potential to survey benthic conditions and communities more rapidly than conventional sampling. This model is used almost exclusively to assess and predict benthic community responses to human disturbances throughout LIS (and has been and is being throughout the world). There were also some surveys in Fishers Island Sound (Zajac 1998a).

The characteristics of soft-sediment infaunal communities in LIS have been reviewed previously by Zajac (1998b) and Zajac et al. (2000a and 2000b) based on broad-scale surveys conducted from the mid 1950s through the 1980s, primarily studies by Sanders (1956), McCall (1975), Reid et al. (1979), and Pellegrino and Hubbard (1983). These analyses showed that benthic communities in LIS show significant spatial variation at several spatial scales. There is a gradient in species richness and community structure along the west to east axis of the Sound. Species richness is relatively low in the western and central basins of LIS, although there are areas that appear to have higher richness; these coincide with coarser sediments (**Fig.** 25). Species richness starts to increase more regularly across habitats on the eastern side of the central basin and in the area of the Mattituck Sill, is somewhat lower beyond this transition zone among sedimentary environments (see Geology chapter) and then increases sharply east of the Connecticut River. The large-scale, east to west gradient likely reflects to some degree a larger potential species pool at the eastern end of LIS and the connection to the open coastal waters of Block Island Sound and the Atlantic Ocean. In central and western LIS, lower species richness may reflect a smaller pool of potential species that have entered the Sound proper, but also a smaller set of species that can successfully maintain populations. Patch and smaller-scale spatial differences in species richness may be related to the sediment characteristics of specific patches with lower richness in muddy sediments and higher richness in sandy and coarser sediments (**Fig.** 26). Furthermore, species richness may be affected by small scale, physical and biogenic habitat characteristics (e.g. Hewitt et al. 2005) but interactions between small-scale habitat structure and species richness are not well known for LIS.

Analysis of data collected by Pellegrino and Hubbard (1983), Zajac (1998b) and Zajac et al. (2000a and 2000b) showed that benthic community structure in LIS varies from west to east, exhibiting several spatial transitions that are related to the large-scale sedimentary and benthic landscape features of the LIS sea floor (**Fig.** 27). Based on classification (clustering) analysis, eleven community types were recognized and several of these exhibited sub-community groups. In the depositional, muddy habitats of the westerns and central basins of LIS, three main types of benthic communities were recognized, dominated by species such the polychaetes *Nephtys incisa* and *Cistenoides gouldii*, and the bivalves *Mulinia lateralis, Nucula annulata and Pitar morrhuana*, differing mostly in terms of relative number of these dominant species. These communities correspond to a mud assemblage identified by Reid et al. (1979) that spanned the central and western basins of LIS and the Narrows in the far western LIS, and are similar to the *Nephtys* - *Yoldia* community identified by Sanders (1956) in the central basin. Another community type dominated by the polychaetes *Clymenella zonalis* and *Mediomastus ambiseta* and the bivalve *Mulinia lateralis* was also found in some muddy areas, especially along transitional areas among different sedimentary environments in east-central LIS. Several types of benthic communities were found in more hydrologically dynamic areas with coarser sediments. A community type dominated by several polychaetes including *Asabellides oculata* and *Spiophanes bombyx*, and the bivalve *Tellina agilis* was found in the transition between the eastern and central basins and along the bathymetric highs separating the central and western basins and Narrows (**Fig.** 27). A community dominated by the polychaetes *Cirratulis grandis, Cirratulis cirratus, Prionospio heterobranchia, Prionospio tenuis*, and the amphipod *Aeginnia longicornis* was found in sandy sedimentary environments in the eastern basin. Areas characterized by primarily coarse-grained sediments contained communities dominated by several species of tubiculous amphipods and polychaetes. These analyses were based on data that were collected only in the CT waters of LIS and as such may not provide an accurate depiction of deeper water benthic assemblages along the southern axis of LIS. We can extrapolate that benthic communities are similar in the portions of specific patches that were not sampled by Pellegrino and Hubbard (1983) to the extent that sedimentary habitats are not excessively different. However, Reid et al. (1979) identified a sand assemblage along the north shore of Long Island that was in shallower waters and as such there is likely more variation in benthic community structure in the transitional areas among the deeper water muddy basins and these sandy areas along this shore.

In summary, studies conducted prior to about 1985 provided a general understanding of composition and structure of the sea floor communities of LIS, and provided a disturbance / response model that could be used for environmental assessment and understanding, in part, the temporal dynamics of these communities.

6.5.1.2 Studies from 1985-2010

Between 1985 and 2010, there were several important developments in the study of seafloor habitats of LIS and their ecology. Central among these was the integration of geologic surveys of the LIS sea floor and studies of the Sound's benthic ecology, which provided the basis and framework for beginning to understand the structure and dynamics of the LIS benthos relative to multi-scale spatial structure and characteristics of the benthic landscape in LIS. [See Geology chapter]. Between the late 1980s and mid 1990s, collaboration among researchers at the US GS, CT DEEP and the University of New Haven began to integrate sea floor mapping and benthic community studies in several deep water sections of LIS (Figs. 28 and 29). This work revealed that sea floor habitat / patch structure can be an important determinant of benthic community structure at small ($\leq m^2$), meso (10s to 100s of m^2) and large scales (> 100s of m^2), and the sea floor mapping has provided the ability to analyze benthic community structure in habitats that could not be easily located, for example the transition zones / ecotones between different types of sedimentary and hard substrate habitats, and sedimentary habitats that have varying geomorphological characteristics (Zajac 1996, 1998a; Zajac et al. 2000, Zajac et al.

2003). These studies also suggested that benthic community responses to disturbances such as hypoxia may be spatially complex (**Fig.** 30) and that successional stages in the Rhoads et al. (1978) model (**Fig.** 24) may not hold in all areas of LIS (Zajac 1998a, 1999, 2001). Maung (2010) recently showed that benthic responses to hypoxia are complex relative to geochemical dynamics at the sediment water interface.

Concurrent advancements in mapping benthic habitats and integrating them with ecological studies were made in the nearshore habitats of LIS over this period (see section on Intertidal and Nearshore Benthos). Building on the increase in sea floor and habitat mapping in the Sound and the growing appreciation of the value of integrated benthic mapping and ecological studies, Auster et al. (2009, see EPA LISS website) developed a Habitat Classification Model for LIS, which can be applied as a framework for continued integration of these types of studies.

The sea floor mapping data in conjunction with several of the benthic study data sets have provided the framework for also beginning to assess the application of marine and coastal spatial and conservation planning in LIS. Neely and Zajac (2008) showed that potential conservation planning scenarios in LIS would be constrained and shaped by the strong physical, chemical and biological gradients in LIS, and conservation scenarios would need to recognize and incorporate such gradients. When calculating necessary conservation areas that would include the diversity of species and community types, they showed that different solution areas were needed in the western vs. eastern portions of LIS due to the spatial heterogeneity of richness and community type distributions noted above.

During this period there have also been several Sound-wide benthic survey / monitoring studies, specifically the EPA Environmental Monitoring and Assessment Program (EMAP) and the National Coastal Assessment (NCA) program (**Fig.** 29). These studies sought to assess the environmental quality of estuarine and coastal areas of the United States and as such their focus was regional. The data collected included benthic community structure, sediment chemical composition, and other environmental characteristics as well as sediment toxicity tests of sediments collected at sampling sites. Using the EMAP data from LIS, Schimmel et al. (1999) assessed the relative degree of impacted vs. non-impacted sites based on a benthic index comprised of a species diversity measure and the abundances of tubificid and spionid annelids. Their analyses suggested that the western deep water portions of LIS were impacted, as were some deep water sites in the eastern portion of LIS as well many harbors and large embayments.

6.5.1.3 Factors Controlling Benthic Community Structure and Dynamics

Most of the benthic studies in LIS have centered on sedimentary habitats, and we know little of the structure and dynamics of communities that inhabit deep-water hard substrates in LIS (e.g. rock outcrops, boulders, gravel patches). These comprise the least plentiful type of habitat by area, but likely add substantively to the overall biodiversity of LIS. There have been few studies of this type of habitat (Liebman 2007), and more are needed.

6.5.1.4 Science Gaps and Management Implications

Although there has been a relatively substantial effort to study the benthic ecology of deep-water portions of LIS, there remain significant gaps in our knowledge. In particular, the temporal dynamics of these communities are not well understood, both with respect to yearly seasonal fluctuations, and longer year-to-year dynamics. Many of the surveys noted above sampled the benthos at specific stations just once and as such it is difficult to interpret changes that are noted from data obtained decades apart without a good understanding of shorter-term fluctuations. For example, Zajac and Whitlatch (in preparation) analyzed the benthic data collected as part of the EPA EMAP and the NCA Programs which span 3 year periods about a decade apart (early 1990s and early 2000s), and found that there were several significant changes in benthic abundances and species richness of the central and western basins of LIS. However, Zajac (1998a) found that in these areas there is significant seasonal and interannual variation in benthic community structure over a two-year period that was approximately of the same magnitude of the decadal changes found by Zajac and Whitlatch (in preparation). Although the EMAP and the NCA programs sampled over three to four years, samples were only taken once a year and not in the same locations as the focus of these programs was to assess regional status of estuarine conditions and not necessarily within-estuary dynamics. As such, we are missing data that are critical to understanding not only the basic dynamics of benthic systems in LIS, but also to assessing temporal changes that may occur in the face of various types of human and natural disturbances and longer-term climate change. There have been no studies of the deep water (nor shallow water) benthic communities that have assessed seasonal and year to year changes for periods greater than 2 years, nor studies that have assessed recovery following disturbance for more than that time span. Benthic disturbance succession models (**Fig.** 24) predict that recovery periods may be on the order of the life span of the species that characterize endpoint, “climax” communities. At least in the deep-water mud environments of LIS these potentially include species such as the polychaete *Nephtys incisa*, maldanid polychaetes, and various bivalves such as *Pitar morrhuanus* and *Mercenaria mercenaria.* These species are among those expected in climax communities; all have potential life spans > 3 years. Studies of these communities and populations of key species are necessary to parse the various spatial and temporal patterns of variability so that any long terms signals and trends can be identified accurately and with confidence. Furthermore we effectively have no information on successional dynamics and endpoint communities in the coarser grained habitats of LIS, and indeed these may be quite different form that characterized in **Fig.** 23 (see Zajac 2001 for an extended discussion of this point). There have been few follow-up studies after certain types of impacts such as pipeline construction that have assessed long-term impacts of these types of disturbances. Finally, and quite surprisingly, there is no long-term, consistent monitoring of benthos inside and out of hypoxic zones, which is critical to understanding long-term impact of seasonal hypoxia and how this may interact with changing climate, such as increasing water temperatures that may exacerbate seasonal hypoxia.

Food web dynamics are key to understanding the overall ecology and ecosystem dynamics of various environments in LIS. To that end data on biomass and productivity of all food web components are necessary. Unfortunately very few data of this type (e.g. Carey 1962, Kroeger 1997) are available for benthic species in LIS, and as such comprise a significant unknown in terms of having LIS specific data that can be incorporated into food web models (Zajac et al. 2008). Future benthic studies in LIS should routinely quantify the biomass and to the extent possible productivity of dominant taxa found in the habitats sampled.

Currently, there is significant effort to continue sea floor habitat mapping studies in LIS. The production of sea floor maps showing detailed bathymetry, sediment type and other features needs to be paired with benthic ecological studies of areas being surveyed, mapped and characterized as sea floor maps alone without associated ecological information will potentially provide little value for understanding and managing these environment alone. In addition, a greater focus on systematic mapping and conducting ecological surveys of inshore benthic environments along both the CT and NY coasts of LIS is strongly warranted.

Many of these information needs could be addressed by establishing sites that would be consistently monitored within the context of a "natural experiment" design (**Fig.** 31). The locations of the benthic monitoring areas would be based on the premise of a "natural experiment" testing spatial difference in community structure at multiple scales and allowing temporal changes (as might occur with climate change) to be assessed in a variety of benthic habitat types across the estuarine gradient in LIS. Within these locations, there would be coordinated physical and chemical monitoring, and detailed habitat mapping, thus providing an ecosystem-based approach to understanding long-term system behavior. A similar shallow water set of monitoring areas could also be established. The areas shown in **Fig.** 31 are suggested sites that include a variety of sedimentary habitats that are repeated along the west - east gradient of LIS and would allow for understanding benthic ecology relative to sediment type and in relation to the gradients of physical and chemical conditions in the Sound.

As we move into the next quarter century, the effective stewardship of this invaluable resource will depend on a much better understanding of all its ecological components. The deep water benthic habitats of LIS are one of these critical components, but yet our understanding of the taxa that reside there, their population and community dynamics, and their contributions to ecosystem function lags far behind the gains we have made over the past 20-25 years with respect to our knowledge of the physical and chemical nature of the estuary, and certain pelagic components. As such it is critical that a more concerted and systematic effort is placed in research so as to close this gap in our overall understanding of LIS.

6.5.1.5 Benthic Disturbance

6.5.1.5.1 Overview and Natural Disturbance

Nearshore and subtidal benthic habitats in LIS are frequently affected by anthropogenic and natural disturbances. Disturbances may be physical (disruption of surface sediments, covering with a layer of mobilized sediments, mixing or sorting of surface sediments, covering with rock or physical structures, shading from physical structures), chemical (anoxia or hypoxia in overlying water, loading of contaminants from water or particle deposition), thermal (exposure to unusually low or high air or water temperatures) or biological (settlement or growth of larvae or adults in sufficient density to alter surface or subsurface conditions). Disturbance of relatively stable sediments or hard bottom substrates is thought to be sufficiently important to benthic habitat structure and function that it provides the driver for several models of benthic succession and community structure (**Fig.** 32) (Sanders 1969; Pearson and Rosenberg 1979; Rhoads et al. 1978; Rhoads and Germano 1986; Zajac 2001). The frequency and degree of disturbance varies widely but generally is expected to decrease with increasing water depth. Shallow water and intertidal habitats are expected to experience high frequency disturbance (tidal exchange, subhourly temperature fluctuations, storm induced salinity change and wave and current disturbance with periodicities measured in seconds). Subtidal habitats may experience tidal current exchange, seasonal disturbance from storms or temperature, but most disturbances occur with periodicities measured in months or years. Most subtidal habitats in LIS are well protected from frequent natural disturbance with the exception of areas scoured by tidal currents near the Race or on shallow ridges or shoals (e.g. Stratford Shoal, Long Sand Shoal). However, the tidal exchange of sediment across the sediment-water interface can be quite substantial in many of these subtidal habitats.

The seasonal influx of suspended sediment into the Sound has been estimated to be 9.3 x 10^8 kg yr^{-1} (Farrow et al. 1986, Rhoads 1994). This is equivalent to an annual sedimentation rate of 0.05 gm $cm-^2$ yr^{-1} based on a total area of 3200 km^2 and 1792 km^2 of fine-grained sediment (Bokuniewicz and Gordon 1980). This estimate compares with long term sedimentation rates determined by ^{210}Pb profiles from the center of LIS of 0.05 gm $cm-^2$ yr^{-1} and radiocarbon dating results of 0.077 gm cm^{-2} yr^{-1} (Benoit et al. 1979). There is evidence that this rate may be higher (0.1 gm $cm-^2$ yr^{-1}) in the western basin (Bokuniewicz 1988). In addition to the influx of suspended sediment, the central and western basins are subject to tidal resuspension and deposition of large volumes of sediment (Rhoads et al. 1984). Most of this resuspended sediment is trapped below the pycnocline in summer and creates a transitory near-bottom turbidity zone (Rhoads et al. 1984). Average near-bottom turbidity values of 5 mg L^{-1} result in an estimate of 2.5 x 10^8 kg or 27% of the annual supply in suspension with higher values in spring and early summer (Bokuniewicz 1988; Rhoads 1994). The flux of sediment due to suspension and redeposition appears to be much higher than the net long-term sedimentation (Rhoads 1994). Using McCall's sediment trap data, Rhoads calculated that 1 x 10^{12} kg of fine sediment were resuspended annually or the equivalent of 1000 times the long term sedimentation rate (McCall 1977; Rhoads 1994). These measured and estimated rates suggest that the benthic environments in the central and western basins experience very high fluxes of fine grained sediments and that very little of the net influx of sediment is removed from the resuspension cycle (Rhoads 1994). The benthic community in these environments is therefore exposed to, and presumably adapted to, relatively high exchange of sediment across the sediment-water interface despite the apparently protected conditions (McCall 1977). During certain storm events the resuspension levels may be much higher, but there is little evidence that storm events are a major source of disturbance except in shallow nearshore habitats.

6.5.1.5.2 .Dredging and Dredged Material Disposal

Dredging affects channel floor habitats, with minimal loss of suspended sediments to surrounding, usually shallow habitats (Bohlen et al. 1979; Wilber et al. 2007). Material removed during dredging is frequently placed on the seafloor in open water habitats with immediate, short-term effects on the benthic community (Germano et al. 1994; Bolam and Rees 2003). The annual average dry weight of dredged material placed in LIS has been estimated at 4.1 x 10^8 kg yr^{-1} or less than half of the annual sedimentation rate (Rhoads 1994). Of this amount, dispersal losses from passage through the water column and resuspension after placement are estimated at 6%, or about 3% of the annual non-disposal sediment input (Rhoads 1994).

Historically, dredged material disposal in the Sound occurred at many sites located just outside harbors adjacent to the recognized channel (Fredette et al. 1993). As a result some benthic habitats still retain traces of placement of isolated piles of harbor sediment (Poppe et al. 2001, 2010; ENSR 2007).

Disposal is now confined to designated disposal areas between 1-2 nm² (nautical miles^2) in deeper areas of LIS (Fredette et al. 1993). Disposal of dredged sediments is permitted for materials that are determined to be suitable for unconfined open water disposal based on biological based testing protocols (Fredette and French 2004; EPA/USACE 1991). Disposal of dredged material typically consists of seasonal placement of 10-500,000 cy (cubic yards) of harbor sediments at buoys by releasing the material from a split-hull barge at the surface. Each barge contains between 500-3,000 cy of water-laden sediment. Recent seafloor imaging studies, experimental placement and laboratory experiments have clarified the physical processes involved in placement of dredged material in open water (Figure 33, Valente et al. 2012; ENSR 2007). The sediment released from the bottom of the barge falls rapidly to the seafloor, entraining some water but retaining a coherent mass until it contacts the seafloor. Upon contact, the vertical force of the bolus of water-entrained sediment is transferred to lateral forces and rapidly spreads in a circular pattern to form a low mound or crater shape on the seafloor (Figure 34). Depending on the water depth, volume of the barge, the water content of the dredged material and the seafloor surface, this mound or crater is between 50-300 m in diameter. This process of sediment placement creates a disturbed sediment surface that consists of a coherent layer of dredged material 10-200 cm thick in the center of the mound thinning to mixed layers of ambient sediment and fresh dredged material. At the outer margin of the placement feature, layers 1-2 mm thick of fresh dredged material can be detected with sediment profile imaging techniques (Germano et al. 2011). This process of placement is usually repeated 10-250 times at a single disposal buoy during a disposal season (October-May) resulting in a shallow mound 1-5 m thick and 200-1500 m in diameter (Figs. 33 and 34, Valente et al. 2012; ENSR 2007).

After placement of sediments on the seafloor, the resulting mound consolidates and remolds over a period of months due to processes of self-weight consolidation (loss of pore water as individual sediment particles settle; Silva et al. 1994; Poindexter-Rollings 1990), bioturbation, and erosion and deposition from near-bottom flow processes (Rhoads 1994). As a result the volume of the mound will decrease and the surface will smooth and begin to converge with conditions of adjacent ambient sediments. The degree of convergence will depend on water depth, physical conditions of the placement site and the differential between placed and ambient sediments (Rhoads 1994). Management of placement sites for containment of dredged material dictates creation of stable mounds in depositional environments that experience a net increase in surface sediment (Fredette and French 2004).

Mounds containing dredged material that is deemed unsuitable for unconfined placement due to elevated levels of contaminants are engineered to meet regulatory guidelines under which the contaminants are rapidly rendered harmless (Fredette and French 2004; EPA/USACE 1991). Studies of the stability of these engineered or “capped” mounds (mounds constructed to isolate the unsuitable material beneath a sediment “cap”; Palermo 1991) have demonstrated that pore water exchange of contaminants with the overlying ambient water is well below background levels (Bokuniewicz 1989; Murray et al. 1994). Longer-term studies of mounds have demonstrated that once the rapid consolidation phase has been completed (ca. 1 year) the surface layers of sediment (10-30 cm) are the only horizons available to interact with biological resources (Fredette et al. 1992; Murray et al. 1994).

The consequence to benthic habitats of the placement of dredged material has been studied in LIS for over 40 years (Fredette and French 2004; Valente 2004). The nature of the impacts can vary depending on the composition of the dredged material and the habitat at the disposal site (Bolam et al. 2006). A structured monitoring approach of disposal impacts has been utilized in LIS since 1977 as part of the Disposal Area Monitoring System, or DAMOS (Germano et al. 1994; Fredette and French 2004). Based on the results of DAMOS studies and the understanding of the physical processes described above, the benthic disturbance that results from placement of dredged material in open water habitats in LIS is a remobilization of surface sediments, burial of surface sediments and benthic infauna, and introduction of disturbed sediments with high organic loads into discrete areas (Germano et al. 1994). Virtually all benthic infauna are smothered in layers that exceed 15 cm. There is a broad range of experimental research which suggests that the ability to escape a given depth of burial from native sediments is related to the life habits of the fauna (Kranz 1974; Maurer et al. 1986; Kjeilen-Eilertsen et al. 2004); strong burrowing deposit feeders can escape from 10 cm or more of burial (Jackson and James 1979; Bellchambers and Richardson 1995) but attached epifaunal suspension feeders cannot survive more than 1 cm (Kranz 1974). This means that some organisms can burrow up through thin layers of fresh sediment, but many will not. The center region of the disposal mounds formed in the Sound are usually sufficiently thick to catastrophically bury all organisms that cannot move quickly (Germano et al. 1994)

An “apron” of thinner material can extend 100-500 m beyond the bathymetrically detectable margin of the mound (accumulations greater than 10 cm can be reliably detected with multibeam surveys, greater than 20 cm with single beam fathometers (Fredette and French 2004; Carey et al. 2012). In the apron of thinner deposition, the introduction of high organic loads provides a surge in potential food supply for deposit feeders and rapid bioturbation usually obliterates the distinct layer within months (Germano et al. 2011).

The surface of the mound, including the apron, attracts high settlement densities of small surface deposit feeders (polychaetes, amphipods, bivalves and meiofauna). This response has been documented by numerous monitoring studies in LIS and is consistent with the successional model of Rhoads et al. (1978) and Pearson and Rosenberg (1978). The nature and rate of recolonization can be strongly influenced by the timing of disturbance relative to seasonal pulses of settlement and growth of larvae (Zajac and Whitlatch 1982; Wilber et al. 2007). The successional model of response to physical disturbance from placement of dredged materials (Rhoads et al. 1978) has been tested with observation of disposal mounds in LIS since 1982 with the use of sediment profile imagery (Germano et al. 2011). Sediment profile imaging (SPI) utilizes a cross-sectional image of the upper 20 cm of the sediments to observe visual evidence of organism-sediment interactions. A phenomenological model (Rhoads and Germano 1982, 1986) has been used to interpret the ecological effects of dredged material in LIS (Germano et al. 1994) and minimize the impacts of disturbance (Fredette 1998; Fredette and French 2004).

The infaunal successional model (Rhoads and Germano 1986) posits that stage 1 organisms (small, tube-dwelling surface deposit feeders) will appear within days or weeks of physical disturbance or deposition of a fresh layer of dredged material. If no further disturbance occurs, these stage 1 organisms are replaced by infaunal deposit feeders (stage 2) and eventually by larger infaunal deposit feeders (stage 3), many of whom feed in a head-down orientation that creates distinctive feeding voids (Germano et al. 2011). The establishment of this mature community may take months to years to complete and results in a deepening of the bioturbated mixed sediment layer and convergence with the surrounding benthic habitat conditions depending on factors such as the spatiotemporal structure of the species pool (Zajac 2001). Potential variation in the rate of succession is illustrated by recent results collected from a disposal mound five months after cessation of disposal in 2009 (Figure 35).

Benthic disturbance from dredged material disposal in LIS has been documented to have immediate effects on sessile epifauna and infauna (Germano et al. 1994, 2011). The management approach to dredged material disposal in LIS includes biological testing of sediments and active management of disposal to segregate materials determined to be unsuitable for unconfined open water placement (Fredette and French 2004; Carey et al. 2006). During the development of the management approach, dredged material known to contain elevated levels of metals and PAHs was placed at the Central Long Island Sound Disposal Site in 1983 at several locations (capped and uncapped) as an experiment and monitored extensively for more than twenty years (Germano and Rhoads 1984; Myre and Germano 2007). Short-term biological effects were observed after placement of unconfined dredged material (Myre and Germano 2007). This joint USEPA/USACE Field Verification Program was designed to field-verify existing test methods for predicting the environmental consequences of dredged material. The biological testing and resulting management approaches (sequestering dredged material with evidence of biological effects beneath a ‘cap’ layer of material without significant biological effects) have contributed to the lack of observable long-term ecological effects from disposal activities in LIS. Apart from alterations of habitat due to introduction of different grain-size composition or changes in sediment transport conditions due to elevation of the seafloor, there is no evidence of long-term effects on benthic processes or habitat conditions (Germano et al. 2011).

6.5.4 **Benthic Foraminifera of LIS**

Foraminifera are unicellular, heterotrophic eukaryotes in the super-group Rhizaria, characterized by a branching, anastomizing network of granular reticulopodia (Adl et al. 2005). Many species have a proteinaceous theca, but many others make a shell (test) by agglutinating mineral grains in an organic or mineral matrix or by secreting $CaCO_3$. Tests may consist of one or many chambers. The life cycle usually comprises alternation between diploid asexually reproducing agamonts and haploid sexually reproducing gamonts. Foraminifera are marine, living from brackish coastal regions to the deepest ocean trenches (Pawlowski and Holzmann 2008).

There are about 50 species of living planktonic foraminifera and several thousand benthic ones (Murray 1991; 2006; 2007). Foraminifera are part of the meiobenthos, i.e., mostly between 63 and 1000 um in diameter. Benthic foraminifera are most diverse (hundreds of morphological species) along the lower continental shelf (Culver and Buzas 1982; Gooday 1993). Estuaries usually contain a few tens of species at most, coastal salt marshes and mangrove forests about 15 species, with 5-10 dominant species (Murray 1991, 2006; Scott et al. 2001; Javaux and Scott 2003).

Classical taxonomy is morphological, based on test material and shape (e.g., Sen Gupta 1999), with genetic information becoming available only recently and for few species (e.g., Holzmann and Pawlowski 1997; Holzmann et al. 1998; Holzmann 2000; Holzmann and Pawlowski 2000; Pawlowski 2000; Hayward et al. 2004; Pawlowski and Holzmann 2008; Schweitzer et al. 2010). Many morphological species have large biogeographic ranges (e.g., Scoptt et al. 2001), dispersing widely due to propagules produced during sexual and asexual reproduction (Alve and Goldstein 2009), but in shallow waters morphotypes do not overlap with genetic groups (e.g., Holzmann and Pawlowski 1997; Hayward et al. 2004; Schweizer et al. 2010).

Foraminifera are ubiquitous in the marine realm, their tests are easily fossilizable, and their small size makes it possible to obtain statistically valid data using relatively small samples (e. g., Jorissen et al. 2007). Planktonic and benthic foraminiferal fossil assemblages thus have been used widely to reconstruct environmental changes on timescales from millions of years (e.g., Thomas 2007) through historical times. In coastal regions, profound changes in foraminiferal faunas occurred at last in part in response to anthropogenic changes (see e.g., Alve 1995, 1996, Alve and Murray 1995; Culver and Buzas 1995; Karlsen et al. 2000; Scott et al. 2001; Platon et al. 2005, Murray 2006, Sen Gupta and Platon 2006, Nikulina et al. 2008, Gooday et al. 2009). In LIS, foraminifera have been used to study salt marsh foraminiferal ecology and reconstruct relative sea level rise, and to study estuarine foraminiferal ecology and eutrophication.

6.5.4.1 Foraminifera in Coastal Salt Marshes of LIS

The distribution and relative abundance of foraminifera in intertidal marsh settings is primarily controlled by physico-chemical conditions related to the fraction of time that the salt marsh surface is not covered by sea water (Scott and Medioli 1978, 1980; Scott et al. 2001). Exposure time is controlled by the elevation of the salt marsh surface above mean sea level and the tidal range, so that marsh foraminifera are distributed in vertical zones, similar to marsh vegetation (Scott and Medioli 1978, 1980; Scott et al. 2001; Horton and Edwards 2006). The zones can be expressed in vertical distance from mean high water (MHW). In high and middle marsh, benthic foraminifera live on the marsh surface or in the topmost 2.5 cm of the sediment, whereas in the low marsh they are dominantly found in the upper 5 cm but with a significant number of living specimens down to 15 cm (Saffert and Thomas 1998; Edwards et al. 2004a).

Dominant foraminifera in coastal salt marshes are agglutinants, constructing tests from mineral and/or biogenic grains (e.g., quartz, mica, diatom frustules) (Bradshaw 1968; Scott et al. 2001; de Rijk 1995). The most common species along the coasts of LIS are *Trochammina macrescens*, *Trochammina inflata*, *Tiphotrocha comprimata*, *Haplophragmoides manilaensis*, *Miliammina fusca*, and *Arenoparrella manilaensi*s. Less common are *Siphotrochammina lobata, Balticammina pesudomacresens, Polysaccamina ipohalina, Pseudothurammina limnetis,* *Ammotium salsum*, *Ammoastuta inepta* and *Textularia earlandi*. *Trochammina macrescens, T.*

inflata, and T. comprimata are the most abundant in middle to high marsh regions, with *H. manilaensis* increasing in relative abundance at lower salinity, and *A. mexicana* close to creeks (Medioli and Scott 1980; Thomas and Varekamp 1991; Nydick et al. 1995; de Rijk 1995; Saffert and Thomas 1998; de Rijk and Troelstra 1999; Scott et al. 2001; Edwards et al. 2004a). Lower in the intertidal zone *M. fusca* is more common, with *A. salsum* and/or *Ammoastuta inepta* at lower salinities. On lower intertidal mudflats the calcareous species *Ammonia parkinsoniana*, various *Elphidium* species, and *Haynesina germanica* may occur (**Fig.** 36).

Salt marsh communities are linked to the duration of tidal inundation, so that coastal marshes are sensitive to changes in sea level (e.g., Donnelly and Bertness 2001). Foraminiferal assemblages are indicative of the elevation of the marsh surface above mean sea level, so that fossil assemblages in core samples can be used to indicate the position of each sample with regard to mean sea level when the foraminifera were living. By dating the samples we can reconstruct the rate of sea level rise over the time of deposition of the samples (Scott and Medioli 1980; Thomas and Varekamp 1991; Varekamp et al. 1992; Nydick et al. 1995; Varekamp and Thomas 1998; Scott et al. 2001; Edwards et al. 2004b; Horton and Edwards 2006), and marsh foraminifera have become the dominant method for evaluating sea-level variation (Armstrong and Brasier 2005). The accuracy of these estimates depends on the width of the foraminiferal zones, thus on the tidal range, and on the exact location of the living foraminifera on or in the sediments (Saffert and Thomas 1998).

With recent rapid sea level rise, New England salt marshes underwent dramatic shifts, with the low marsh species *Spartina alterniflora* replacing the high marsh *Spartina patens* (Thomas and Varekamp 1991; Varekamp et al. 1992; Warren and Niering 1993; Nydick et al. 1995; Varekamp and Thomas 1998; Thompson et al. 2000; Donnelly and Bertness 2001;

Edwards et al. 2004b; Fitzgerald et al. 2008). Ultimately, loss of salt marsh is expected, and has been observed (Donnelly and Bertness 2001). Benthic foraminifera thus can be used to monitor the ability of salt marshes to adapt to increasing rates of sea-level rise.

6.5.4.2 Subtidal Foraminifera of LIS

Foraminifera from western LIS and New York Harbor were first described by Shupack (1934), followed by more detailed studies in the late 1940s (Parker 1952), and an exhaustive study in the 1960s (Buzas 1965), with additional data analysis by Murray (1976). The morphology of the dominant *Elphidium* species was studied by Buzas (1966), Miller et al. (1982), and Buzas et al. (1985). Thomas et al. (2000) described assemblages collected in the 1990s. Thomas et al. (2004, 2009, 2010, 2011) compared data on assemblages from grab samples (i.e., recently living) with assemblage data on core samples representing the last millennia (Thomas et al. 2004, 2009, 2010, 2011; Varekamp et al. 2010).

LIS faunas are 'marginally marine', with a low species richness and diversity (e.g., Murray 1991; Scott et al. 2001). Abundant species have high tolerances for fluctuations in temperature, oxygen levels and salinity, and environmental pollution (e.g., Moodley and Hess 1992; Alve 1995; Culver and Buzas 1995; Gooday et al. 2009). Foraminifera are common to abundant in most of LIS, with the exception of areas of coarse sand, sediment erosion, non-deposition and transport i.e., east of 72.6 ^{o}W (Hammonassett) (Knebel and Poppe 2000).

The most frequent species in LIS (**Fig.** 37) (Parker 1948; Buzas 1965; Thomas et al. 2000) are the calcareous hyaline *Elphidium excavatum*, *Elphidium incertum*, *Buccella frigida*, and *Ammonia parkinsoniana* (formerly described as *A. beccarii*, or *A. beccarii* s.l.), and the agglutinated species *Eggerella advena* and *Trochammina squamata*. Rare species (< 5%) include the agglutinated *Rheophax scorpiurus, Rheophax nana* and *Textularia earlandi,* the calcareous hyaline *Lagena* spp., *Dentalina* spp., *Nonion commune*, *Buliminella elegantissima*, *Fursenkoina fusiformis, Bolivina* spp., *Hopkinsina* sp., and *Polymorphina novangliae,* the epiphytic species *Cibicides lobatulus* and *Cornuspira planorbis,* and the calcareous porcellaneous *Quinqueloculina* spp. The rare species are more common in eastern LIS than towards the west, and they were more common in the 1960s (Buzas 1965) and earlier (Parker 1948) than they are today (Thomas et al. 2000). Species characteristic for coastal salt marsh environments are found in LIS close to the shore, but not as living specimens.

The most common morphospecies in LIS belong to the genera *Elphidium* and *Ammonia* and display wide morphological variability (e.g., Schnitker 1974; Miller et al. 1982). There are no simple correlations between morphotypes and genotypes (e.g., Holzmann et al. 1996, 1998; Holzmann and Pawlowski 1997, 2000; Holzmann 2000; Hayward et al. 2004; Schweizer et al. 2010). The *Ammonia* species in LIS was formerly named *A. beccarii* (e.g., Thomas et al. 2000), but genetic information shows this is incorrect for the LIS genotypes (Pawlowski et al. 1995; Holzmann et al. 1996, 1998; Holzmann and Pawlowski 1997;Hayward et al. 2004). The name *Ammonia parkinsoniana* is used until more genetic information becomes available (Holzmann and Pawlowski 1997; Hayward et al. 2004). The most common *Elphidium* species in LIS is assigned to the species *E. excavatum*, but has been named *E. clavatum* or *E. clavatum excavatum* in the past (e.g., Miller et al. 1982; Buzas et al. 1985). There is no genetic information available, but German representatives of this species group belong to distinct genetic types (Schweizer et al. 2010).

In LIS, Buzas (1965) recognized an assemblage with >60% *E. excavatum* at depths from 3-19 m (average 11 m), an assemblage with common *E. excavatum*, >9% *B. frigida* and <19% *E.*

advena at 15-33 m (average 26 m), and a third assemblage with >19% *E. advena* at 19-39 m depth (average 30 m). *Ammonia parkinsoniana* was rare (<5%). The most abundant species remained the same in the 1990s (Thomas, 2000), but assemblages differed profoundly from these in the 1960s by the establishment of an east-west rather than a depth zonation, with *Ammonia parkinsoniana* common to dominant (up to 85%) in westernmost LIS (Thomas et al. 2004, 2009, 2010, 2011). This is a highly significant change: core studies show that *E. excavatum* was the dominant foraminiferal species in shallow water settings since the establishment of LIS (Thomas et al. 2004, 2011; Varekamp et al. 2010), and that *A. parkinsoniana* began to increase in abundance in the late 1960s to early 1970s in westernmost LIS, spreading eastwards (Thomas et al. 2004). In addition, in the 1990s the relative abundance of *E. advena* which had in the deeper part of LIS been >19% (Buzas 1965) plummeted to a few percent at most (Thomas et al. 2000, 2004, 2010). Core studies show that it was more abundant before the 1800s, declined in abundance in the early 20th century, increase shortly in the early 1960s, followed by a continued decline (Thomas et al. 2004, 2011) (**Fig.** 38).

Buzas (1965) suggested that the assemblages might be controlled by food supply, with the *E. excavatum*-dominated faunas in the photic zone feeding on benthic algae and diatoms. Murray (1991) described *E. excavatum* as an herbivore, and *E. advena* as a detritivore (Alve 1995). *Elphidium excavatum* consume diatoms and can sequester their chloroplasts, thus becoming functional photosynthesizers, giving them competitive advantage over heterotrophs in sunlit waters (Lopez 1979; Lee et al. 1988; Lee and Lee 1989; Lee and Anderson 1991, Bernhard and Bowser 1999; Pillet et al. 2011). *Elphidium excavatum* also sequesters chloroplasts in aphotic waters, where they might help in survival during hypoxia (Cedhagen 1991), and increasing feeding efficiency (e.g., Bernhard and Bowser 1999).

The ecology of *Elphidium incertum* is not well known; it flourishes in quiet waters without strong current activity. Little is known about the ecology of *Buccella frigida*, which is common in fine-grained, organic-rich sediments rich (Murray 1991, 2006). The agglutinated *Eggerella advena* survives under low oxygen and severely polluted conditions, but is relatively sensitive to low salinity (Murray 1991; Alve 1995). *Ammonia parkinsoniana* is cosmopolitan, omnivorous (Bradshaw 1957), survives wide swings in temperature and salinity, and is abundant in highly polluted regions (Murray 1991, 2006; Alve 1995).

6.5.4.3 Causes of Foraminiferal Faunal Change in LIS

The foraminiferal faunal changes in core records in the early to middle 1800s consist of increased relative and absolute abundance of *E. excavatum*, possibly caused by eutrophication which led to increased diatom productivity from the earliest 19th century on (Varekamp et al. 2010). The first decline in relative abundance of the agglutinated species *Eggerella advena* at that same time may have been caused by decreasing salinity (Varekamp et al. 2004, 2009, 2010), as documented by stable isotope studies of benthic foraminiferal tests. A short-term increase in salinity (and the relative abundance of *E. advena*) occurred during the drought years in the 1960s (Buzas 1965).

Abundance of *Ammonia* species relative to *Elphidium* species is commonly expressed as the *Ammonia*-*Elphidium* index (A-E index, Figure 39), which has high values in eutrophied, hypoxic waters (e.g., Chesapeake Bay and the Gulf of Mexico; Sen Gupta et al. 1996; Karlsen et al. 2000; Platon et al. 2005; Sen Gupta and Platon 2006; Gooday et al. 2009). Increased abundance of *Ammonia* spp. thus has been tentatively explained as caused by hypoxia. We see correlation between hypoxia and high abundance of *Ammonia* spp., but do not interpret this as causation: both *E. excavatum* and *A. parkinsoniana* are extremely resilient under hypoxia, and survive full anoxia for several days (Moodley and Hess 1992). Regional rise in water temperatures could be a contributing factor, because *Ammonia* species are more common in warm waters than *Elphidium* species (Murray 1991, 2006), and needs several weeks of temperatures above 20^o C for efficient reproduction (Bradshaw 1957). It is, however, improbable that warming is the main factor causing the rise in abundance of *A. parkinsoniana*, because temperatures are not very different in western and eastern LIS.

A more probable cause for the decrease in abundance of *E. excavatum* may be a decrease in overall bulk diatom productivity, as seen in biogenic silica records (Varekamp et al. 2010), possibly resulting from low N/Si values during severe eutrophication. This may have led to declining relative abundances of the specialized diatom consumer *E. excavatum* (Varekamp et al. 2005). Limited genetic evidence on the genus *Ammonia* in LIS, however, allows the possibility that the recent increase in relative abundance was caused by an invasive cryptospecies (Holzmann and Pawlowski 1997; Hayward et al. 2004).

In conclusion, benthic foraminifera have been used to document ecosystem changes over time, and may be used in the future to monitor possible ecosystem changes due to changes in climate and nitrogen input (Gooday et al. 2009).

6.6 Fish, Shellfish, and Wildlife

6.6.1 Finfish Communities and Fisheries

LIS oceanography is driven primarily by openings to the Hudson Raritan Estuary through the East River and through an opening to the Atlantic Ocean at the eastern end through "the

Race”. The Sound ecosystem is characterized by habitats ranging from tributary streams, emergent and regularly flooded marshes and open estuarine to fully marine waters. The total volume of LIS is 64×10^9 m^3 over an area of 337,000 ha (Wolfe et al. 1991), of which approximately 84 km^2 are tidal marshes and freshwater and brackish tributaries (Long Island Sound Study 1994, 2003). The temperature and salinity of the sound varies seasonally, but averages 11.2ºC and 27.3‰ (See Physical Oceanography chapter; Gottschall et al. 2000). The estuarine waters of LIS are nursery and feeding grounds for over 100 species of resident and migratory finfish (Gottschall and Pacileo 2010). The variety of bottom types, water depths, currents and tide ranges found in different parts of LIS create a myriad of habitats for a large array of species. This diversity of species has supported ecosystem functions and commercial harvest for centuries.

Glaciers retreated from Long Island and Connecticut coasts between 17,000 to 20,000 years ago, leaving a large freshwater lake that filled with seawater when sea level rose creating, the ecologically rich estuarine sound (Bernstein 2006). Occupation by native people has been verified for the past 12,000 years, although 2000-3000 years ago permanent settlements along the coast in bays and estuaries were maintained by hunter-gatherer-fisher cultures (Bernstein 2006). First nation’s people were primarily dependent on fish and shellfish close to shore. Remains of shell middens suggest heavy use of hard clam and oyster, and lesser consumption of soft clam, bay scallop and some knobbed whelk (Witek 1990), that appears to have been close to year-round harvest (Lightfoot and Cerrato 1988). Early accounts describe fishing through use of torchlight with spears and clubs, nets, hooks, bow and arrow, traps, and weirs in the LIS region (Banks 1990). Weirs were constructed using wooden stakes driven into the river bottom, occasionally supported by rock walls in areas of swift current, where water level receded in low tides (Banks 1990). Stakes were interwoven with branches to create a barrier that confined fish such that they could be captured by dipnet or spear (Banks 1990). Relicts of these structures remain today in many of the river mouths which drain to the Sound.

Anadromous fish provided the greatest density of available food for societies in the Hudson Valley (Fisher 1983), and capture of anadromous species in Connecticut is supported by a number of stake weirs in the Housatonic River and their common use throughout the eastern United States (Lutins 1992). Thus, the primary fish species captured by native cultures around LIS would have included, in order of likely importance: American shad, American eel and lamprey, and also alewife, blueback herring and Atlantic salmon. Long Island Native Americans were also known as skilled whalers, although it is not clear if pre-contact populations simply scavenged whales when they stranded (Merwin 1993).

In the early 1600s, Dutch colonists settled around New York (New Amsterdam at the time) and along the Sound’s shoreline discovering abundant fish and mammals in the nursery areas of the numerous marshes and small tributaries. Lucrative fur and fish trading enterprises were initiated, with the beaver a prime target. Interactions between the first nations and colonists initially were peaceful, but war over these valuable resources was inevitable. The Dutch West Indies Company maintained control over much of the fish trade around the region, of which details are scant, until the English took over in 1664. Trade documents indicate that the Dutch imitated the native cultures’ consumption of herring, possibly fueled by religious beliefs that limited meat in their diet, and an export monopoly of pickled herring allowed the Dutch to enjoy substantial wealth (Matthews 1927). However, even though the primary fish species exported by the Dutch was herring, local consumption by the colonists was probably the same fish and shellfish species as native cultures enjoyed. Initially, dead or stranded whales were a coveted resource and provided revenue and materials for entire towns if found (Ross 1902).

Initially, much of the region was farmland and in order to boost production fish were added to the fields in the fall. Atlantic menhaden was of critical importance in this regard. Starting in the 1600s, menhaden were taken in small quantities from small bays, inlets and river mouths in shallow water using simple gear (Hathaway 1910). While menhaden were primarily used as fertilizer here, they were consumed by poorer inhabitants in the southern US (Hathaway 1910). Menhaden were an important fertilizer on Long Island by the 1700s, with the claim that it doubled land value (Ross 1902). Seaweed, seagrass and marsh grasses were also used (Ross 1902), and mussels were recorded as used for fertilizer in the early 20th century (Matthews 1927). Menhaden form vast schools during migrations between northern feeding and summer spawning habitats, which could be easily landed by haul seines drawn ashore by horses. Millions of pounds were harvested every year.

During the 1650s, Long Island whalers became engaged in the expanding commercial rendering of oil, an extremely valuable commodity, such that between 1670 and 1850 whaling was considered “the great trade on the Long Island coast” (Ross 1902). Cold Spring Harbor had 9-10 ships engaged in whaling in 1843 although the number of whales harvested from LIS is unknown. However, by the late 1800s whaling trips had become a multi-year effort, with ships sailing as far as the Pacific Ocean (Ross 1902). In 1850, the extraction of oil from menhaden was developed on an industrial scale. Until 1870 the menhaden harvest was relatively small, but the need for oil combined with the loss of whales as a local resource created a new fishery that persists until the present time. The ease with which the menhaden could be caught with purse seines and quickly brought to nearby factories fueled a very lucrative fish oil industry that replaced whale oil as a critical Long Island commodity. In 1881, over 200 million fish were harvested and rendered into over a million gallons of fish oil in Southport alone (Ross 1902). From 1885 to 1910 annual United States menhaden catches ranged from about a quarter million in 1892 to over one million pounds in 1903 (Hathaway 1910). In 1910, menhaden were still considered a coastwide resource but had disappeared from the Gulf of Maine (Hathaway 1910). Modeling of the adjacent Great South Bay system demonstrates they played a critical ecosystem role at the turn of the century in the Long Island region, both as a filter feeder and forage fish for top predators (Nuttall et al. 2011). Thus, over the past 100 years, the role of both menhaden and top predators such as the sand tiger shark were dramatically reduced within inshore bays, and loss of migratory species significantly changed energy flows within and among food webs (Nuttall et al. 2011).

The past century saw the advent of industrialization and with it unprecedented human impacts on the shores and waters of the Sound. To date, 25-35% of the Sound’s tidal wetlands have been lost due to dredging, filling and development (Long Island Sound Study 1994, 2003). The loss of wetlands increases from east to west, directly related to pressures of urbanization (Long Island Sound Study 2003). Increasing environmental perturbations related to industrial pollution began to have an effect on the Sound’s animal populations. Poor water quality accelerated the mortality of the Sound’s oysters such that the annual harvest declined from 10 million pounds in 1957 to less than 1 million pounds by 1960 (Bureau of Commercial Fisheries 1963).

Several diadromous species also declined primarily due to industrial dams but also declining water quality (Limburg and Waldman 2009; Hall et al. 2011). There are over 1000 dams in the Connecticut River watershed, although only six mainstem dams play a role in anadromous fish declines and restoration. Mainstem dams at Enfield in Connecticut and Holyoke and Turner’s Falls in Massachusetts embody historic fish passage issues. The first mill dams were erected throughout Atlantic coastal watersheds during the early 1600s, however the technology required to span larger rivers was not available until the late 1700s. Permanent obstructions were in place by 1798 at Turners Falls 120 miles upriver, 1849 at Hadley Falls 87 miles upstream, and the 1827 Enfield Dam at 65 miles upriver. These dams provided power to industry but more importantly produced navigable waterway by bypassing flow through lock systems and increasing water depth above the dam sufficiently to allow transport of goods (Cumbler 1991).

The success and failure of fish passage projects since 1800 have ebbed and flowed in response to local litigation due to the effects of floods and spring freshets (Ducheney et al. 2006). In 1801, the westerly end of the Holyoke Dam was torn down to alleviate flooding of local properties, and at the same time restoring fish passage. A new dam downstream of the original was constructed in 1815, and accompanying litigation forced a fishway to be built 4 years later. An 1824 freshet destroyed the dam and necessitated construction again, but only after a period of obstruction until the owner was found guilty of preventing upstream fish passage. As a result of this litigation the dam was altered again to allow passage. In 1866, the Commonwealth of Massachusetts enacted legislation requiring free passage of shad and salmon on the Connecticut River. In 1873, a wooden fish ladder was constructed on the Holyoke Dam, but no fish used the ladder and in 1895 the Massachusetts legislature passed an act that exempted Holyoke Water Power from the need of maintaining a fishway. The current dam at Holyoke was built in 1900 and in 1938 the act exempting fishway maintenance was repealed. In 1940, a second ineffective fish ladder was constructed. In 1955, a fish elevator at Holyoke Dam provided some passage, which was further improved in the 1970s when a fish ladder was also constructed at Turners Falls. The Enfield Dam fell into disrepair in the late 1970s and is presently breached thus allowing full passage, although many people are petitioning for its reconstruction.

Fish passage targets identified by the Connecticut River Atlantic Salmon Commission and required in the 1999 Holyoke Dam FERC license include 1,000,000 American shad, 1,000,000 blueback herring, 6,000 Atlantic salmon, 500 shortnose sturgeon, and an unspecified number of American eel (Ducheney et al. 2006). Salmon were considered plentiful in 1797, but few remained in 1808 and none by 1820 (Cumbler 1991). Although in 1849 seines could still catch over two thousand shad in a single sweep, numbers declined after 1820 and disappeared completely from the upper river in the 19th century. Eighteen fifty marks a decrease from 40,000-50,000 shad landed annually to less than 35,000 afterwards (Cumbler 1991). During the late 1800s artificial propagation became widespread. For example, rearing ponds between 1896 and 1910 provided 57,029,000 shad fry stocked into the Connecticut River (Moss 1965). Seth Green had been commissioned to hatch shad and in 1868 had released what he had estimated to be about 40,000,000 shad fry in the Connecticut River (Moss 1965). Restoring salmon runs has been far more difficult because salmon were extirpated from state waters in 1820. A native stock had to be reconstructed using wild and farmed salmon from Maine and Canada that were released into the Connecticut River. Returning fish have contributed to the distinct Connecticut River strain since 1979, and 100s of millions of young parr and smolt have been released into the river since 1970 (USASAC 2011). However, to date the number of returning salmon captured at various river monitoring locations has never exceed 530 (USFWS 2011).

6.6.1.1 Shellfish Aquaculture

Historically, natural oyster beds were a prominent feature along the coast of Connecticut, both shores of Long Island, all of Manhattan Island and up the Hudson River as far as the saltwater extended (Matthews 1927). LIS was among the first areas to be heavily exploited for its wild shellfish resources; by the late 1700s oyster catches were already declining (EOBRT 2007). Oyster Bay enacted fishing seasons for oysters in 1801 suggesting that supplies were being threatened, and in 1807 allowed ownership of bottom ground for the production of oysters (Ross 1902). Dredges were introduced in some areas in the early 1800s, and catches declined even more rapidly despite strong demand (EOBRT 2007). By 1855, natural oyster reefs had been reduced to such little value that they were used only for the seed they produced (Matthews 1927) and East River oystermen began to use clean shells to catch the seed of oysters, so that they could be transplanted for growth to market (Matthews 1927). During the same period a fishery for scallops developed in the Sound, with a large fleet dredging the bottom during fall and winter months. Oyster production was limited due to low demand after peak landings in 1910 until 1938 when production was impacted by a major hurricane that covered many beds with sediment and destroyed harvest vessels (MacKenzie 1997). Beds were again destroyed by a hurricane in 1950 and inadequate supplies limited oyster production until the mid-1980s (MacKenzie 1997).

Investment in pollution abatement projects since the 1970s has aided a rebound of aquaculture in the Sound (LIS Study 2003). Production was also greatly increased by massive private and government cultch plantings during 1988-1991 (MacKenzie 1997). The majority of the oysters in the region currently are produced in Connecticut waters. From 1990 to 1996, an average of 643 thousand bushels of eastern oysters and 129 thousand bushels of northern quahogs (hard clam) were harvested annually from cultured beds in Connecticut waters alone, worth \$26-49 million in market value annually (CT DOA Division of Aquaculture landings data). In 1997-1998, a disease die-off in the Sound's oyster beds caused the annual oyster harvest in Connecticut to drop 10-fold, from 526 thousand bushels in 1996 to 56 thousand in 2001 (CT DOA Division of Aquaculture landings data).

Eastern oysters display a wide range of survival strategies because they inhabit a naturally variable environment; they are both colonizers and ecosystem engineers and have a high reproductive potential (OEBRT 2007). In the years following the die-off, CT DOA Aquaculture Division staff and federal aquaculturists at the NOAA laboratory in Milford, CT, worked with industry to introduce disease resistant strains of seed oysters (Rawson et al. 2010). Oyster harvest rates have slowly increased, but remain well below the peak harvests. In recent years the industry has turned to hard clams to fill the gap left by the loss of oyster harvest, as well as the loss of lobster harvest, in western LIS. By 2007, 48.9 million hard clams, and 13.5 million oysters were harvested by Connecticut license holders, worth a total of \$25.7 million in market value. Farm-raised shellfish in LIS is presently supplied by approximately 40 companies concentrating on oysters and hard clam. Attempts to restore oyster populations and rebuild the resource through general cultch planting, reef rebuilding and oyster sanctuaries/reserves are also becoming common management tools (OEBRT 2007). However, the industry has learned the hard lesson that depending on the culture of a single species can lead to catastrophic loss from disease or predation, and is working hard to diversify aquaculture efforts. Experimental culture operations have been initiated for blue mussels, razor clams, macroalgae (*Porphyra spp.*) and bay scallops for restoration purposes (Getchis 2005). Currently, 271 km^2 of LIS seabed is leased Rfor aquaculture that generates more than \$12 million (Getchis 2005), using techniques almost unchanged for 200 years.

6.6.1.2 Lobster Trap Fishery

The wild harvest of lobster in LIS is second only to shellfish aquaculture in total revenue. From 1880-1892, 0.6-0.7 million kg of lobster were landed annually and represented the highest state landings from Connecticut until 1983 (Blake and Smith 1984). Annual landings declined by 50-90% through the 1950s (Blake and Smith 1984). Landings began to slowly increase in the late 1960s as a trawl fishery and subsequent trap fishery moved offshore and encountered abundant lobster in offshore grounds (General Dynamics 1968). By the late 1980s trap landings were further bolstered with the replacement of the traditional wooden lathe trap with the vinyl clad wire trap which proved much more durable and efficient. The advent of this gear upgrade, and regulations prohibiting the targeted harvest of lobster by trawlers in the Sound due to the damage this gear causes to lobsters (Smith and Howell 1987), changed the fishery from principally a part-time or mixed-species endeavor to a full time single-species industry. By the late 1990s, landings from LIS peaked at 5.3 million kg, supporting over 1,000 license holders and generating $ 36 million in ex-vessel value (CT DEP 2000; NY DEC unpublished data). Historically, 50-60% of this harvest occurred in western Sound waters (CT DEP 2000). A massive die-off that occurred in the fall of 1998 and intensified in 1999 impacted the productive western Sound waters most severely with landings declining by more than a third in one year (CT DEP 2000). Individual ports suffered even greater losses, particularly in the Narrows, where landings in the port of Greenwich fell 70% while Norwalk declined 48% and Stamford dropped 43% in 1999. A decade later much of the lobster harvest activity was gone in these ports and the remnant lobster population was concentrated in the deeper waters of the central basin and the Race (See Lobster Die-Off section later in this chapter).

6.6.1.3 Finfish Trawl and Gill-Net Fishery

Springtime signals American shad migration from the Sound up Connecticut’s major rivers to spawn. The commercial shad fishery takes advantage of the migration ‘run’ by tending drift gill-nets in the river’s current to entrap the fish. This fishery peaked in the mid-1800s but continues today with a handful of drift gill-net fishermen. The Connecticut River shad population, the largest in the state, fell to only 16,000 spawning adults in 1967 when a federally coordinated restoration program was started by the US Fish and Wildlife Service. Thirty years later, after rigorous water quality programs were put in place and fishways allowed the fish to migrate past major dams to preferred spawning grounds, the population reached 300,000 spawning adults (USFWS 2011). Automated counters installed in the Holyoke Dam fishway now provide a quick means of monitoring the spawning population which has been stable at 156,000-168,000 fish from 2006-2010 (USFWS 2011) after the fishery harvested 30,000-50,000 (CT DEP MFIS 2010) fish for traditional springtime shad bakes.

Although landings from the trawl fishery earn less than a quarter of the annual revenues that come from aquaculture and the lobster fishery, trawl-caught finfish have been the main source of locally harvested seafood since the invention of coal-fired steam engines in the early twentieth century (CT DEP MFIS 2010). By the early 1900s, diverse net and long-line fisheries exploited the swift currents in the Race targeting bluefish, mackerel and menhaden (Ross 1902). It is difficult to precisely track harvest of individual finfish species solely from LIS because catches landed in LIS ports do not necessarily mean the fish were caught within the its waters. Much of the Sound’s harvest has been landed at out-of-state ports since the 1960s (Blake and Smith 1984), and harvest from elsewhere is routinely landed at ports around the Sound.

However, landings data are an essential tool used by fisheries scientists and managers to track trends in harvest and provide evidence of ecosystem dynamics.

CT DEP landing reports were highest in the mid-1990s and have declined over the past decade (**Fig.** 40, CT DEP MFIS 2010). Since the 1960s, commercial finfish landings have been dominated by summer flounder (fluke) and winter flounder, and these two species are also the most valuable (CT DEP MFIS 2010). Historically, winter flounder was also among the most abundant species in LIS, but this species has experienced a drastic decline in both landings and value since the late 1990s (CT DEP MFIS 2010). Conversely, scup (porgy) was traditionally considered of low value, but since 2003 demand and value of this species has increased (CT DEP MFIS 2010, **Fig.** 41).

The economic value of Connecticut commercial finfish and shellfish landings has been monitored by CT DEP since 1978. Data for Connecticut show that the ex-vessel value of total landings steadily increased from a few million dollars before 1980 to a record high value of over $61 million in 1992, boosted by increasingly large shellfish landings (CT DEP MFIS 2010). Despite declines in total weight harvested, the overall value of total landings has generally increased, providing over $30 million to harvesters annually since 2005 (CT DEP MFIS 2010). These figures represent only the value of these landings at the dock. The total economic impact of commercial fishing on the Sound’s coastal communities is far greater.

6.6.1.4 Recreational Fisheries

Recreational fishing became an important pastime beginning in the late 1800s and into the early 1900s, as fishing and hunting clubs cropped up targeting some 200 species of salt- and freshwater fish (Ross 1902). In more recent years, recreational fishing activity in LIS has remained steady at around 1.5 million trips each year since 1981 (**Fig.** 42). Recreational landings peaked in the early 1980s and have declined by nearly 50%, likely due to a combination of regulatory restrictions and declines in some important resident species. The most popular species targeted in the Sound are bluefish, striped bass, scup, summer flounder (fluke), and tautog (blackfish). In several species, the reported catches from recreational fisheries are considerably greater than commercial landings. For striped bass and bluefish in particular, the recreational fishing is almost an order of magnitude greater than the commercial landings, showing that these species primarily experience recreational harvest (MacLeod 2009). In recent years, anglers caught over 10 million fish of all species each year, but kept less than a third of their catch (MacLeod 2009; NYDEC unpublished data). The best comprehensive estimate of the economic value generated by current recreational and commercial fishing activities in LIS is $5 billion per year towards the economy of the region (LIS Study 1994).

6.6.1.5 Trends in Abundance, Diversity, and Community Structure

Although parts of the Sound's finfish community have been documented for centuries in commercial and recreational catch records as well as research studies, the most comprehensive data set, in spatial coverage and duration, is the CT DEEP LIS Trawl Survey (LISTS). The survey has been conducted each spring and fall since 1984 and utilizes a stratified-random sampling design with fixed strata of 1 x 2 nautical miles (Gottschall and Pacileo 2010). A total of 40 stations are conducted each season using a 14 m bottom trawl with a 51 mm cod end towed for 30 minutes. The survey is used to identify species, community and ecosystem dynamics on spatial and temporal scales and provides the primary data for management and scientific investigations related to the Sound's finfish and shellfish.

The overall abundance of finfish captured by the survey has remained relatively stable since 1984 with an increase observed in the fall and a decrease in the spring (**Fig.** 43). In the first five years (1984-1989) of the Survey catch rates in spring and fall were nearly identical; however, in the last five years (2003-2008), they were almost an order of magnitude different. Over the time series (1984-2008), the most commonly captured species in the fall were butterfish, scup, long-finned squid, weakfish, bluefish, anchovy, windowpane flounder, winter flounder and little skate (**Fig.** 44A). Of the top ten finfish species significant increases in abundance were observed for butterfish (r = 0.4, p <= 0.042), scup (r = 0.6, p <= 0.001), weakfish (r = 0.6, p <= 0.001) and anchovy (r = 0.5, p <= 0.013), while significant decreases were observed in abundance for windowpane flounder (r = -0.5, p <= 0.005) and winter flounder (r = -0.5, p <= 0.022). The top ten species captured in the spring included winter flounder, scup, windowpane flounder, American lobster, butterfish, little skate, long-finned squid, Atlantic herring, fourspot flounder and red hake (**Fig.** 44B). Of the ten most abundant finfish species increasing trends were observed in scup (r = 0.5, p <= 0.009), and butterfish (r = 0.54, p <= 0.005), while decreasing trends were observed for winter flounder (r = -0.7, p <= 0.001), windowpane flounder (r = -0.8, p <= 0.001), little skate (r = -0.4, p <= 0.033), fourspot flounder (r = -0.6, p <= 0.001) and red hake (r = -0.4, p <= 0.037).

In addition to changes in individual species, large-scale changes have been observed in multi-species groups representing different habitat use and ecological guilds. All of the finfish species captured by the survey (**Table**s 5 and 6) were grouped into species that are bottom tending (epibenthic, n=36), species that prefer the upper water column (pelagic, n=35) and species that utilize both benthic and pelagic habitats (demersal, n=24). Spring catches have been dominated by epibenthic species, although their abundance has declined significantly since 1984

($r^2 = 0.67$, $p < 0.001$; **Fig.** 45). At the same time the abundance of demersal species significantly increased ($r^2 = 0.24$, $p = 0.007$) though with large variance. The abundance of pelagic species showed no trend. However, it should be noted that the bottom tending gear used in the survey may under-sample these species and may not have the statistical power to detect trends. Fall abundance data showed a greater increase in demersal species ($r^2 = 0.44$, $p < 0.001$) than is seen in spring catches, while fall abundance of the other two groups showed no trend.

In order to identify important sub-groups in the trends observed for demersal, epibenthic and pelagic species, the abundance trends of flatfish, skates and shellfish were estimated. The aggregate abundance trends for the 30 most common species were analyzed for the following groups: demersal (scup, silver hake, tautog, spot, black seabass, weakfish), skate (little skate and winter skate), shellfish (American lobster), epibenthic (striped searobin, red hake, northern searobin) and flatfish (windowpane flounder, winter flounder, fourspot flounder, hogchoker, summer flounder, smallmouth flounder). In both seasons flatfish and skate have declined, while demersal species have increased, especially in the fall (**Fig.** 46). The increase in demersal species is driven largely by scup, while decreases in flatfish were driven by winter flounder, windowpane founder and fourspot flounder. Epibenthic abundance decreased in the fall and increased in the spring, while American lobster increased in the 1980s until a decline in the 1990s.

The decline in spring abundance was not accompanied by a decline in overall finfish species diversity (**Fig.** 47). Diversity in spring catches has remained fairly steady over the 25-year time series, averaging about 11 species per sample, while diversity in fall catches has increased, rising from about 11 species per sample to 13. Epibenthic species continue to be about twice as commonly captured in the survey as demersal and pelagic species.

6.6.1.5.1 Spatial Trends

The LIST Survey is designed to randomly sample 12 spatial habitats: three bottom types (sand, mud, and transitional between the two) at four 9.1 m water depths. Average catches over the time series among these 12 habitat types ranged from 27 fish per sample at deep sand sites, primarily found mid-Sound west of the Connecticut River mouth, upwards to an average of 99 fish per sample at mud sites in the western basin at mid-depths of 20-30 m. This spatial pattern has remained fairly constant over the 25-year time series.

Although the spatial distribution of the finfish community has not changed, research trawl catch data indicate individual species shifts and a general trend towards decreased flatfish abundance that appears to stabilize after 1999. A multivariate analysis was completed that only considers species that were caught in over 40% of tows in order to remove the influence of highly migratory species whose affinity to a specific habitat or species group cannot be well supported (see Jordaan et al. 2010). Bootstrapping and principal component analysis (PCA) were applied using a correlation matrix, with 16 and 17 species in the analysis of spring and fall data, respectively. The 3 PCs account for 48% and 45%, and the top 5 PCs explain 63% and 58% of the total variance for spring and fall survey data, respectively. PCA scores for individual sites were then interpolated using inverse-distance weighting and contrasting species groups shaded in light (negative scores outside 1 standard deviation) and dark (positive scores outside 1 standard deviation). Thus, species groups can be visualized as 3 sets (PC1, PC2 and PC3) of contrasting species groups (**Fig.** 50). A further challenge is that many species are at historic low abundances and have undergone further rapid population declines during the time period of the LISTS survey (Limburg and Waldman 2009). The results indicate increasing habitat differentiation and organization from spring to fall (**Fig.** 50), a result shared by other temperate systems (Jordaan et al., in press). Temperate regions face a fall-winter overturn, forced by cooling surface waters relative bottom temperature, and storms/ice conditions that deconstruct ecological structure followed by an annual re-organization. Biological activity often peaks with reproduction and population expansion during spring blooms, and this is followed by a summer growth season. In the fall, species spatially segregate into western, west-central, east-central and eastern groups, and also along depth contours, to create a mosaic of assemblage groups (**Fig.** 50). The ecological structure identified is consistent with expectations that the westernmost Sound experiences lower oxygen levels and other environmental characteristics that differ from the central basin, a remnant of the post-glaciation lake. The Race region in the easternmost Sound, in contrast, experiences higher water velocity and less anthropogenic impacts other than fishing pressure. The ecological structures of both the eastern and western regions do not appear to relate to depth, suggesting more homogeneous habitat characteristics than the central regions. It is important to note that these results do not include analyses of species dynamics such as predator-prey relationships and their interaction with climate and fishing. A full ecosystem modeling exercise would better elucidate key ecological processes.

6.6.1.5.2 Seasonal Trends

These seasonal trends hint at community-level changes made clearer when species captured in the survey are grouped by habitat use, or ecological guilds (**Table**s 5 and 6): The composite abundance trend of species that live on the bottom (epibenthic, n=36) was compared to the composite trend of species that prefer the upper water column (pelagic, n=35) and species that utilize both benthic and pelagic habitats (demersal, n=24). Spring LISTS catches are dominated by epibenthic species, however their abundance has declined significantly since 1984 (**Fig.** 45). At the same time the spring abundance of demersal species has significantly increased, though showing large annual variance. The abundance of pelagic species showed no trend. However, it should be noted that the bottom tending gear used in the survey may under-sample these species and may not have the statistical power to detect trends. Fall LISTS abundance data showed a greater increase in demersal species than is seen in spring catches, while fall abundance of the other two groups showed no trend. In order to identify important sub-groups in the trends observed for demersal, epibenthic and pelagic species, the abundance trends of flatfish, skates and shellfish were examined separately. In both seasons flatfish and skate declined, while demersal species have increased, especially in the fall (**Fig.** 46). The increase in demersal species is driven largely by scup, while decreases in flatfish were driven by winter flounder, windowpane founder and fourspot flounder.

It is important to note that the decline in spring LISTS abundance was not accompanied by a decline in overall finfish species diversity (**Fig.** 47). Diversity in spring catches has remained fairly steady over the 25-year time series, averaging about 11 species per sample, while diversity in fall catches has increased from about 11 species per sample to 13. Epibenthic species continue to be about twice as commonly captured in the survey as demersal and pelagic species.

These research trawl catch data can also be used to track individual species habitat shifts using multivariate (principal component) analysis (see Jordaan et al. 2010). Finfish species caught in at least 40% of survey tows were analyzed using this approach and results indicate increasing habitat differentiation and organization from spring to fall (**Fig.** 48), a result shared by other temperate systems (Jordaan et al., in press). Temperate regions face a fall-winter overturn, forced by cooling surface waters relative bottom temperature, and storms/ice conditions that deconstruct ecological structure followed by an annual re-organization. Biological activity often peaks with reproduction and population expansion during spring blooms, and this is followed by a summer growth season. In the fall, species spatially segregate into western, west-central, east-central and eastern groups, and also along depth contours, to create a mosaic of assemblage groups (**Fig.** 48). The ecological structure identified is consistent with expectations that the westernmost Sound experiences lower oxygen levels and other environmental characteristics that differ from the central basin, a remnant of the post-glaciation lake. The Race region in the easternmost Sound, in contrast, experiences higher water velocity and less anthropogenic impacts other than fishing pressure. The ecological structures of both the eastern and western regions do not appear to relate to depth, suggesting more homogeneous habitat characteristics than the central regions. It is important to note that these results do not include analyses of species dynamics such as predator-prey relationships and their interaction with climate and fishing. A full ecosystem modeling exercise would better elucidate key ecological processes.

6.6.1.5.3 Drivers of Community Change

Community assemblage structure and species distributional changes have been linked to fishing pressure (Fogarty and Murawski 1998), density-dependent waves (Fauchald et al. 2006), food availability (Olsson et al. 2006) and environmental drivers that impact the condition of individuals (Lucey and Nye 2010; Nye et al. 2009; Frisk et al. 2008, 2010). Low dissolved oxygen (hypoxia) has been linked to decreased species abundance in the Sound, with squid and bluefish showing the most sensitivity (Howell and Simpson 1994). Variation of temperature can cause changes in stratification, hypoxia duration and severity, disease prevalence and other indirect effects. Trends in the LISTS show that cold-adapted species have declined in abundance, while warm-adapted species have increased, suggesting that warming temperatures may be altering the LIS finfish community. The decrease of cold-adapted species has been especially dramatic during the spring (Figs. 48 and 49). In contrast, warm adapted and southern migrant species adapted to subtropical and tropical conditions have increased.

6.6.1.6 Science Gaps and Management Implications

LIS is a productive system that has provided an abundance of resources to the suburban and urban populations of Connecticut and New York for over two centuries and to first nation people for 12,000 years. Available data suggests that the system is characterized by species switches important to local fisheries and shifts in finfish community composition. Perhaps the first major shift occurred with the over-harvest of whales and marine mammals in the 18th century, followed by the dramatic decline in anadromous species in the 19th century and the early 20th century coast wide over-harvest of Atlantic menhaden. More recently LIS has seen a dramatic decline in winter flounder and American lobster and increases in warm-adapted species (see Drivers of community change). Climate change and hypoxia have been proposed as modern drivers of change (see hypoxia section), suggesting that the 21st century will also be characterized by large-scale biological flux in LIS.

The LIS finfish community has responded to a warming trend by shifting from one in which cold-adapted species are numerically dominant, particularly in spring, to one in which warm-adapted species are increasingly abundant, especially in fall. Most of these warm-adapted species have historic ranges centered off the mid-Atlantic and a northward shift of these populations to LIS is consistent with trends and forecasts at larger biogeographic scales (Murawski 1993; Nye et al. 2009; Hare et al. 2010). Temperature has been identified as an important factor in reducing the contribution of cold adapted species and increasing the role of warm adapted species in LIS. However, causes of distributional trends in finfish populations can come from many sources and be complex combinations of variables. Mechanisms of community change in LIS remain elusive as a result of a paucity of finfish studies.

Additional mechanisms need to be explored in the Sound to gain insight into the shifts in abundance observed in the survey and in fisheries data. LIS has a long history of seafood harvest that has been well documented as a driver of habitat and community change in the western Atlantic (Fogarty and Murawski 1998, Frisk et al. 2011). The relationship between fishery harvest and system change can be direct, such as the removal of traditional groundfish in the western Atlantic, but can also be indirect and difficult to detect. For example, Atlantic menhaden has recently been identified as a keystone species in the 19th century Great South Bay, New York, ecosystem (Nuttall et al. 2011). The loss of this keystone species and top predators marked the beginning of a century long decline system maturity in the Bay (Nuttall et al. 2011).

The use of seasonal surveys, conducted annually during relatively fixed periods, to decipher community and species shifts in temporal and spatial distribution is a complex and difficult problem (Dunton et al. 2010, Frisk et al. 2008). The Sound has diverse finfish fauna (Briggs and Waldman 2002) that exhibit a wide range of migration behaviors (Latham 1917). Seasonal variation in the abundance of species collected in surveys can be a function of changes in timing of migration due to environmental factors and decadal patterns in species distribution

(Dunton et al. 2010; Frisk et al. 2008). Ecosystem modeling exercises using time-varying parameters such as has been applied to Chesapeake Bay and Delaware Bay (Christensen et al. 2009; Frisk et al. 2011) would be instructive in relating trends observed in surveys and harvest to the biology of the Sound's natural resources.

6.6.2 Lobster Mortality Events in LIS

The American lobster (*Homarus americanus*) fishery has been an important component of New England's economy and culture for hundreds of years. Abundance has waxed and waned over this time, enjoying a large increase in the 1990s. However, in the fall of 1999 the lobster population in LIS experienced an unprecedented mortality event from which it has not recovered. State and federal landings data show that prior to the die-off, Connecticut and New York commercial landings ranged from 7 to 11.7 million pounds annually, with an ex-vessel value of $18 to $40 million. Participation in the fishery peaked in 1998 when over 1200 residents of the two states bought licenses to fish commercially. However, by 2002 fewer than 900 residents purchased licenses and by 2009 that number declined to 592. Commercial landings also plummeted to about 1 million pounds by 2009, with an ex-vessel value under $3.5 million.

6.6.2.1 Historic mortality events

The American lobster ranges from maritime Canada to Virginia, however south of Long Island the species is found only offshore in deep cool water. LIS marks the southern extent of their distribution in warm near-shore waters. As the animals approach the limit of their temperature tolerance, the likelihood of being exposed to stressful conditions increases. Reports of localized small-scale mortality events in the Sound are common, especially during the fall when water temperatures are highest. Periodic larger mortality events have also occurred. For example outbreaks of gaffkemia (*Aerococcus viridans homari*), also known as wasting or red tail disease, occurred in the fall of 1990, 1991, and 1993.

6.6.2.2 The "die-off" in 1999

Beginning in late summer and early fall of 1999, reports of large numbers of dead and dying lobsters of all sizes came in from lobster fishers in the western Sound. Reports of dead and lethargic lobsters in the central and eastern basins of LIS also increased soon after. In western ports, commercial landings declined by over 90% in fall 1999 compared to their 1995-1998 average**.** Reductions in fall landings for ports east of Norwalk, CT, ranged from 64% to 91%. The declaration by the US Department of Commerce of a Fisheries Disaster in early 2000 fueled extensive research and data collection by many academic, federal, and state agencies from 2001-2005. These studies provided substantial evidence that a combination of physical factors pushed the Sound's lobster population far out of equilibrium with its environment in the fall of 1999. Lobsters were subjected to increasingly hostile conditions, which overwhelmed their immune system. Those unable to either cope physically or move into a better environment ultimately died. Although many of these adverse conditions were not new in the Sound, collectively they had never been as severe. The analogy of the "perfect storm" seems the best way to capture the sequence of events. The next paragraphs list a chronology of the most important events, published in greater detail by Connecticut Sea Grant (Balcom and Howell 2006).

6.6.2.2.1 Warm Waters and Hypoxic Conditions

Water temperature affects all of life history processes of American lobster including growth, maturity, spawning, egg maturation, and larval maturation. Southern New England represents the southern extent of the geographic range of this species and water temperature is the primary habitat constraint within this region. American lobsters are capable of detecting temperature changes of 1°C (Jury and Watson 2000), demonstrate a thermal preference of 12 to 18 °C, and will avoid temperatures > 19 °C (Crossin et al. 1998). Water temperatures > 28 °C cause mortality to adult lobsters within 48 hours and more quickly when the dissolved oxygen is reduced below 6.4 mg/L (McLeese 1956). Prolonged exposure to water temperature above 20 °C causes physiological stress as indicated by hemolymph acidosis (Dove et al. 2005), increased respiration rate (Powers et al. 2004), and depression of immune response (Dove et al. 2005; Steenbergen et al. 1978). It has also been linked to increased incidence of disease including epizootic shell disease (Glenn and Pugh 2006), and excretory calcinosis (Dove et al. 2004).

There has been a dramatic and widespread increase in the spatial range and duration of water temperatures above 20 °C in the coastal waters of southern New England. The best illustration of this phenomenon is the marked increase in the number of days each year when the mean bottom water temperature remains above 20 °C, as measured at the intakes of the Millstone Power Station in eastern LIS (**Fig.** 51).

Bottom water temperatures were 1-2^0 C warmer than average for a number of months during 1998-1999 under drought conditions. Although this temperature increase seems small, it exceeded the upper tolerance threshold for lobsters (20^{0}C) for more than 83 "degree days." Temperatures recorded in deep-water areas of the Sound were higher than 21^{0}C by late summer 1999; shallow areas recorded temperatures higher than 23^{0}C. As the water warmed up, oxygen solubility decreased. Hypoxic conditions formed in the western LIS for about 50 days, which was not out of the ordinary. The worst period occurred in the first week of August and most of the hypoxia had dissipated by August 21st. Lobsters are known to "herd" or crowd in high numbers near margins of hypoxic zones where oxygen is slightly less than 2 mg L^{-1}, their normal respiratory threshold. Because of these two factors - water temperature and hypoxia - an already dense population of lobsters was crowded into the few remaining areas of the Sound cool enough and oxygenated enough to sustain them. Those lobsters were then caught in shrinking areas of tolerable conditions and had no escape when their "islands" disappeared.

In August 1999, the water column was stratified by both temperature and salinity. On August 28th, the region felt the effects of Hurricane Dennis to the south, coupled with strong winds from a northern cold front. These clashing weather conditions caused rapid and complete vertical mixing of the water column, bringing warm surface water to the bottom. As a result, deeper bottom water temperatures increased by 1^0C in six hours (from 21 to 22 ^{0}C) in some locations. When tropical storm Floyd passed through on September 16th, dropping more than three inches of rain, the gush of freshwater runoff that followed the storm caused re-stratification of the water column due to a large difference in salinity, trapping the warm water on the bottom.

6.6.2.2.2 Role of Pesticides

The unusually large freshet from storm Floyd also may have flushed pesticides into the Sound from coastal areas of New York and Connecticut where they were sprayed to combat West Nile virus, a new threat in the area. It is clear that lobsters in western LIS would have suffered extensive mortality in 1999 in the absence of any pesticide effects. However, it cannot be ruled out that in limited areas of the far western Sound exposure to pyrethroid pesticides may have further weakened some lobsters, making them even more susceptible to disease or the inhospitable environmental conditions. Lobster larvae, if they were present in these same areas at the time of exposure, also could have suffered. However, larval abundance in the western Sound peaked as usual in early July, according to CT DEP sampling (Giannini and Howell 2010), while most pesticide applications were made later in the summer and fall.

6.6.2.2.3 The Final Effects

The cumulative effects of climatic and oceanographic factors stressed the lobsters to a point where their immune systems could not cope with rapidly changing and increasingly lethal conditions. During the last months of 1999 thousands of lobsters, crabs and starfish were collected dead, or in their weakened state they became infected with parasitic amoebae and then died. Sustained above-average bottom water temperature was the driving force. Other factors collectively compounded the physiological stress of the high temperature.

Mortality events following the 1999 ‘die-off’ have been less wide spread although better documented. Sampling of the commercial catch by CT DEEP and NYS DEC staff has recorded mortalities in all seasons but primarily in the fall. Observations of the Connecticut commercial catch since 1983 show an increase in the incidence of dead lobsters in the five years following the die-off; incidence increased from a very rare event (<1% of the monthly observed catch) to a common one (up to 7% of the monthly observed catch), with individual trips recording mortalities as high as 46%.

6.6.2.3 Abundance Trends and Changes in Distribution

CT DEEP trawl survey data indicate that conditions throughout LIS were favorable for recruitment of small young lobsters in the early 1990's, allowing the lobster stock to increase to historic high abundance (Gottschall and Pacileo 2010). This enhanced survival of young ended abruptly with the die-off. Similar trends were seen in Rhode Island and southern Massachusetts waters, as well as in offshore canyons south of Long Island (ASMFC 2009). Research survey catches in these areas show that abundance of small lobsters increased through the 1990's followed by a decline to record lows. These trends suggest that regional environmental factors were at first favorable and then very unfavorable for lobster production through the 1990s and continuing into the following decade.

Catch data from a lobster trap survey conducted by NYS DEC in western LIS during 2003 showed that lobster catches dropped sharply when bottom dissolved oxygen fell below 4 ppm and water temperatures rose above 18^0C. This drop was particularly noted for egg-bearing females. In 2003 bottom water temperatures recorded in this survey were above 19^o C from mid-August through September. By 2007 bottom water temperatures were above 19^0C from mid-July through September. The highest catch rate in all four years (2003-2007) of the survey was in the deepest water depths sampled (31-35m).

Catch data from the trawl survey conducted by CT DEEP since 1984 (Gottschall and Pacileo 2010) also indicate that there has been a shift in lobster distribution in the central and western basins of LIS. At sites with muddy bottom sediment, preferred habitat for lobster in this area, catches have shifted from shallow inshore waters to deeper mid-Sound waters. In 1984-1991, the mean catch at sites less than 9m deep was comparable to the mean catch at sites deeper than 27m. However, the mean catch in 2000-2008 at shallow sites was less than half the mean for deep sites (**Fig.** 52). It appears that loss of optimal near-shore habitat may be causing the dwindling stock to contract spatially into deeper water. In western LIS, the potential expansion of chronic hypoxia under conditions of higher temperature compounds the physical effects of both factors.

6.6.2.4 Fishing and Natural Mortality

Assessment of the effect of harvest removals on the Sound's lobster population is complicated by the increase in natural losses made obvious during the die-off in 1999 and following years. Catch patterns seen in all southern New England trawl surveys carried out by in state waters by Connecticut, Rhode Island, and Massachusetts and by the National Marine Fisheries Service in offshore federal waters, indicate that non-fishing (natural) mortality increased approximately two-fold beginning in 1997 (ASMFC 2010). Since 1999, harvest removals (pounds landed) and harvest effort (traps fished and licenses sold) in this entire area have decreased substantially, however lobster abundance has not rebounded even to near-average levels. Although lobster stocks north of Cape Cod are thriving, the reproductive potential and abundance of the southern New England stock remains low.

Some of the losses in the southern stock may be due to 'shell disease' or the bacterial breakdown of the lobster's shell forming pits or lesions. First noted in 1997, shell disease has been observed throughout eastern LIS, Narragansett Bay and Rhode Island Sound, and Buzzards Bay and Vineyard Sound. Each year it is observed in about 15-30% of the population, with the highest percentage in egg-baring females. An index of abundance of newly-settled lobsters, measured in Narragansett Bay beginning in 1992, matched subsequent recruitment to the fishery for several years but broke down after 1997 when shell disease first became prevalent in Rhode

Island waters (Gibson and Wahle 2005). Researchers have hypothesized that the supply of new recruits is greatly reduced by the increased mortality due to shell disease.

The history of disease outbreaks and mortality events paints a dire picture for the southern stock of American lobster. However, apparently devastating natural events often have positive as well as negative effects. All of the lethal and sub-lethal factors described above have exerted strong selective forces on the genetics of southern New England lobster stock. Those animals that survive to maturity and successfully reproduce are better suited to their changed environment than those that did not. And if conditions do not change too rapidly, this lobster stock will continue to evolve so that they will be poised once again to take advantage of favorable conditions whenever they may occur.

6.6.3 Wildlife—Marine reptiles, birds, and mammals

6.6.3.1 Marine Reptiles

Sea turtles have been reported in the northeast states including LIS since the beginning of the last century (Murphy 1916; Babcock 1919; DeSola 1931). Surveys for abundance and distribution of sea turtles in LIS have not been conducted with any consistency. The absence of survey data has fostered inaccurate assumptions related to the presence or absence of sea turtles in LIS. Information on animals inhabiting LIS has come from stranding data, opportunistic sightings reported by mariners, and the general public (citizen scientists) (DiGiovanni et al. 2000). These sightings have been supplemented by the occurrence of stranded animals alive and dead over the last three decades. It is the combination of these data that was used to assess presence of animals in the LIS. Few in-situ tracking and diet studies were conducted in the last two decades limiting our ability to determine habitat usage in these areas.

The only tracking data for sea turtles are from studies conducted in the Peconic Bay Estuary during the late 1980s and from animals rehabilitated and satellite tagged by the Riverhead Foundation for Marine Research and Preservation (RFMRP) starting in 2002. Satellite tracking of rehabilitated animals has revealed that sea turtles are using the waters around Long Island on a regular basis (DiGiovanni et al. 2009).

LIS is a seasonal foraging habitat to three species of sea turtles: loggerhead (*Caretta caretta*), Kemp's ridley (*Lepidochelys kempii*) and green (*Chelonia mydas*). These animals enter the coastal waters of the Northwest Atlantic after spending their early years surviving in near surface waters of the North Atlantic Gyre and then move into the coastal environment of the northwest Atlantic. It is in these bays and estuaries that they begin to develop their benthic lifestyle (Morreale and Standora 2005). LIS and the eastern bays of Long Island are critical developmental habitat for loggerhead and Kemp's ridley sea turtles (Morreale and Standora 2005) arriving in early summer and leaving in early fall.

Few studies have addressed the extent to which sea turtles use the LIS as a habitat. Diet studies on sea turtles were conducted during the late 1980s and early 1990s by Burke, Morreale, and Standora on sea turtles captured in the Peconic Estuary and life history and habitat data were collected (Morreale and Standora 1992). These studies revealed a diet of spider crabs (*Libinia emarginata*) and green crabs (*Carcinus maenas*) for Kemp's ridleys (Burke et al. 1991) and for loggerhead sea turtles (Burke et al. 1993 and 1994). The Atlantic green sea turtle (*Chelonia mydas*) is an omnivore during its early developmental years, but as it enters the coastal habitat of the western North Atlantic is becomes more of an herbivore feeding on *Codium* sp. and brown algae. Nesting of sea turtles has not been reported in LIS for any of the species encountered.

Sea turtles begin to show up in the eastern bays and estuaries during late spring or summer. They remain in the area throughout the summer beginning their southward or offshore migration from New York waters in mid-October. If these animals do not leave early enough in the fall they can become cold stunned (hypothermic) and wash up on the beaches around New York and New England.

Cold stunning of sea turtles is a major problem for the Kemp’s ridley, loggerhead and green sea turtles. These animals wash up on north-facing beaches of LIS (Morreale et al. 1992; Burke et al. 1991). Historically, the sea turtle most affected by cold stunning is the Kemp’s ridley. Reports from the early years of the last century described cold-stunned animals washing up in LIS (Latham 1969). They are thought to have been Kemp’s ridley sea turtles. In recent years cold-stunned Atlantic green sea turtles are becoming more prevalent (DiGiovanni unpublished data). This shift could be attributed to more animals using the waters of eastern Long Island and LIS.

6.6.3.2 Birds

LIS is important for three main groups of birds; those found at sea, on coastal beaches and mudflats, and in tidal marshes. Systematic surveys of offshore birds are largely lacking, and with just a few exceptions, comprehensive information on abundance and distribution is limited. More is known about coastal species, and detailed studies have been conducted on several beach-nesting and tidal marsh birds.

Most open water species, such as waterfowl, loons, and grebes, are most common during nonbreeding periods, with few lingering into summer. Congregations of several thousand greater scaup (*Aythya marila*) are common during winter, especially towards the western end of the

Sound.. Detailed studies of their diets (Cronan 1957) and contaminant levels (Cohen et al. 2000) have been conducted. White-winged scoter (*Melanitta fusca*) and brant (*Branta bernicla*) also occur in large flocks, especially during migration, but most other sea ducks are less numerous. Common loons (*Gavia immer*), red-throated loons (*G. stellata*), and horned grebes (*Podiceps auritus*) are moderately prevalent along the Sound's coasts from fall until spring.

Great cormorants (*Phalacrocorax carbo*) also occur primarily during winter, but the closely related double-crested cormorant (*P. auritus*) occurs year-round, with abundance peaks during spring and fall migration, and a growing breeding population. Concerns have been raised over the adverse effects of cormorant increases on their prey, but a study of alewives (*Alosa pseudoharengus*) suggests that cormorant-caused mortality is largely compensatory and is unlikely to impact populations at a regional scale (Dalton et al. 2009).

Although gulls occur year-round, both abundance and variety are greatest from fall until spring. Large congregations occur from late March-early April, when thousands of migrant gulls feed on offshore plankton. These flocks are dominated by ring-billed (*Larus delawarensis*), herring (*L. argentatus*), and Bonaparte's gulls (*Chroicocephalus philadelphia),* but several others species also occur. Herring and greater black-backed gulls (*L. marinus*) both nest in small numbers along the coast. Ring-billed gulls also over-summer, and there is an influx of laughing gulls (*Leucophaeus atricilla*) from further south in late summer. Several species of terns also summer in LIS. The federally endangered roseate tern (*Sterna dougallii*) nests in small numbers on Faulkner's Island and in much larger numbers on Great Gull Island (Spendelow *et al.* 1995). At both sites the colonies are dominated by greater numbers of common terns (*S. hirundo*), which also nest in small numbers elsewhere along the coast.

Pelagic species are much less common, although some – e.g., northern gannets (*Morus bassanus*), razorbills (*Alca torda*) – seem to be using the Sound more often than previously and have become regular non-breeding visitors, especially in eastern LIS. During summer, small numbers of Wilson's storm-petrels (*Oceanites oceanicus*), which breed in the southern hemisphere during the austral summer, can also be found.

The Sound's shoreline is important for a suite of beach-nesting birds, and for nonbreeding shorebirds and gulls. Among the nesting species, piping plovers (*Charadrius melodus*) are perhaps the best studied, and the species of greatest conservation concern. Federally-listed under the U.S. Endangered Species Act, this species and least terns (*Sternula antillarum*) are the focus of management programs to fence nesting areas and discourage human disturbance. Other beach-nesting species include American oystercatcher (*Haematopus palliatus*) and black skimmers (*Rynchops niger*), both of which appear to be increasing. The primary threats to all of these species are trampling of the eggs by people and elevated predation levels due to human activities (Warnock et al. 2001). Nest flooding on high spring tides adds a more natural cause of breeding failure, albeit one that is likely exacerbated by the reduced area of suitable nesting habitat due to coastal development, and that is likely to become a growing problem with rising sea levels.

Locally nonbreeding shorebirds, especially sanderling (*Calidris alba*), forage on beaches seeking prey in wet sand as each wave retreats. Other species, including purple sandpipers (*Calidris maritima*) and ruddy turnstones (*Arenaria interpres*), use rocky shores and jetties where they eat mollusks, crustaceans, and the like. At high tide, these species are joined by a variety of other shorebirds displaced from the mudflats where they forage by probing wet mud for invertebrates. High tide roosts – such as that which forms on the sand bars at Milford Point, CT – can contain thousands of semipalmated sandpipers (*Calidris pusilla*) and numerous other species. Although these roost sites are used only for short periods of the day, the scarcity of disturbance-free sites can make them especially important. The shorebird concentrations at such sites also make them a magnet for predators such as peregrine falcons (*Falco peregrinus*) and merlins (*F. columbarius*).

The last group of birds that depends on LIS's habitats is found in tidal marshes. The primary breeding species include American black ducks (*Anas rubripes*), clapper rails (*Rallus longirostris*), willets (*Tringa semipalmata*), and both seaside (*Ammodramus maritimus*) and saltmarsh sparrows (*A. caudacutus*). Herons, egrets, and glossy ibis (*Plegadis falcinellus*), which mostly nest in colonies on nearshore islands, fly to marshes to forage on small fishes and invertebrates. Breeding ospreys (*Pandion haliaetus*) reverse this commute, nesting primarily on human-built platforms placed in coastal marshes, but flying offshore to hunt for fish. During migration, various other species of shorebirds and ducks are also found.

Historically, habitat for all these birds has declined as tidal marshes were developed and modified through mosquito ditching, tidal restriction, upland development, and invasion by the introduced reed *Phragmites australis* (Bertness et al. 2009; Crain et al. 2009). Tidal marsh habitats today are better protected and considerable restoration work has occurred (Warren et al. 2002). Nonetheless, the threat of rising sea levels associated with a warming climate poses a new threat with potentially dire consequences. The saltmarsh sparrow (*Ammodramus caudacutus),* for example, is already prone to frequent nest flooding and even small increases in relative sea level could seriously impact reproduction and increase extinction risk (Bayard and Elphick 2011). Over time, all species that nest in the high marsh are likely to experience increased nest flooding and ultimately most tidal marsh habitat is projected to convert to either low marsh or mudflat (Hoover 2009).

6.6.3.3 Mammals

Historically numerous marine mammals have used LIS throughout the seasons. These include two groups: cetaceans and pinnipeds. Systematic surveys throughout LIS for marine mammals have not been conducted annually. The only continuous monitoring of marine mammals is conducted during the winter and spring and focuses on pinnipeds. These surveys conducted by the Riverhead Foundation for Marine Research and Preservation since 1997 have documented an increase in harbor seals (*Phoca vitulina*) and gray seals (*Halichoerus grypus*) in the waters around Long Island (DiGiovanni et al. 2009). The peak season for seals in New York waters is winter with animals arriving from northern waters of New England and Canada in the fall and leaving in late spring. Recent data suggest that this season is expanding and more animals are staying in the area year round. Pinniped surveys conducted over the last two decades have revealed an increase in seal population from hundreds of animals in the early 1990s to thousands during the last count during the winter of 2011.

Due to the lack of survey data for cetaceans, data collected via strandings, opportunistic sightings and the NOAA Sighting Advisory System for North Atlantic Right whales (*Eubalaena glacialis*) have been used as baseline. Only if animals were encountered on a regular basis were they thought to frequent LIS. Cetaceans are encountered throughout the year and include bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus delphis*), harbor porpoise (*Phocoena phocoena*), and North Atlantic right whales (*Eubalaena glacialis*). The North Atlantic right whale has been encountered in the eastern portion of LIS. Harbor porpoise have been recovered throughout LIS by the rescue program and sightings have occurred as far west as the East River and Flushing Bay. These reports were collected by the Riverhead Foundation's Sighting Program and verified by photos or biologists from the Foundation. Bottlenose dolphins were reported in western LIS in Huntington Harbor in 2009. This sighting event was of over 100 animals and lasted more than a week.

As these populations were reduced through natural and anthropogenic causes their encounter rate has decreased. As these animals have been protected since the introduction of the marine mammal protection act in 1972 we have started to see an increase in occurrences throughout LIS, from Sheffield Island, Pelham Bay Park, and the north shore of Long Island in the west to Little Gull Island to the east. Over the last two decades harbor seal abundance has increased in these areas. Since 2001, gray seals have been seen on western Long Island haul-out sites and have increased over the last decade (DiGiovanni et al. 2009).

6.7 Cross-cutting Themes and Summary

6.7.1 Biological Contributions to Hypoxia

6.7.1.1 Processes

Significant portions of nearshore marine water columns suffer from varying degrees of dissolved oxygen (DO) depletion, with conditions ranging from hypoxic to fully anoxic/sulfidic. In fact, increasingly large regions of the world's oceans have persistent oxygen minimum zones (OMZs) at intermediate depths, changing the structure and function of marine communities and subsequently altering nutrient cycles, and negatively affecting energy flow to higher trophic levels while compressing their habitats (Rabalais and Turner 2001; Diaz and Rosenberg 2008; Stramma et al. 2008). The expanse and dynamics of OMZs are closely related to human activity and climate change (Hendy and Pederson 2006). Increasing stratification, reduced ventilation and declining gas solubilities due to global warming are expected to shift the global balance between C and O_2, thereby expanding O_2-depleted regions (Keeling and Garcia 2002; Rabalais et al. 2010; Keeling et al. 2010). So-called “creeping dead zones”, driven by eutrophication, are expanding along coasts and in stratified estuaries, such as the Gulf of Mexico, Chesapeake Bay and LIS (Rabalais et al. 2010; Gooday et al. 2009, 2010) and have significant effects on coastal benthic ecosystems (see Biological Consequences of Hypoxia later in this chapter).

Hypoxia has been defined as maintenance of DO concentrations below either 2 or 3 mg O_2 L^{-1} (62 or 94 μM O_2) in bottom waters (Pavela et al. 1983; Parker and O’Reilly 1991; Welsh and Eller 1991). Many regulatory agencies define hypoxia as < 3 mg O_2 L^{-1} because juveniles and adults of many benthic invertebrate and fish species experience physiological stress below this concentration (Ritter and Montagna 1999). Seasonal hypoxia is common to numerous estuaries, such as LIS, Chesapeake Bay, Neuse River to name a few (Gooday et al. 2009), and develops when consumption rates of DO exceed its resupply rates to bottom waters through physical mixing and transport processes (ventilation). Seasonal hypoxia in bottom waters has been observed in the western narrows of LIS (WLIS) since the early 1970’s and some suggest that mild hypoxia dates back to the pre-colonial era (Parker and O’Reilly 1991). Geochemical and micropaleontological core observations show that more severe hypoxia did not pre-date the middle 19th century, however (Thomas et al. 2004, 2009, 2010; Varekamp et al. 2009, 2010). Ever since systematic monitoring commenced in 1987, LIS hypoxia has varied interannually between 78 and 100 km^2 (30 - 390 mi^2) in areal extent and 33-82 days in duration and is highly unpredictable (http://longislandsoundstudy.net). Over the last three decades, hypoxia has occurred annually and usually initiates near Throgs Neck Bridge and propagates eastward to at least the NY- CT border through late summer (LISS 1994). Although monitoring by state and local government agencies dates as far back as 1914, historical trends are unclear because of relatively low spatial and temporal sampling resolution and analytical limitations of early monitoring programs.

Processes controlling hypoxia in the LIS ecosystem have received comparatively little direct study and have been assumed to be much like those of Chesapeake Bay and other major estuaries by modelers and resource managers. Most estuaries originate from a major river and minor tributaries discharging directly to the sea through a drowned river valley, a glacial cut or through a bar-built lagoon. Their circulation is controlled by freshwater discharge rates, geomorphology, and ocean tides in a relatively straightforward manner. However, LIS is distinct from most other estuaries. Today, most freshwater inputs to LIS are orthogonal to the estuary's primary axis, mainly from the Connecticut, Housatonic and Thames rivers and municipal sewage treatment plants (STPs). LIS's unusual hydrography and geomorphology, including three sub-basins formed by two north-south sills, impose limited tidal exchange with the ocean and long hydraulic residence times (Wilson et al., this issue). LIS's complex circulation patterns do not conform to classic salt wedge, partially mixed, vertically homogenous nor inverted circulation models. These unusual attributes make LIS susceptible to strong seasonal physical stratification, especially when vertical mixing by wind stress and thermohaline circulation is minimal. Limited bottom water exchange imposed by stratification is essential for oxygen depletion and the timing, duration and amplitude of isolation contribute to hypoxia dynamics (Welsh and Eller 1991; Vigil 1991; Anderson and Taylor 2001).

In the isolated bottom waters of LIS during late summer and early fall, DO concentrations are drawn down by biological and chemical oxygen utilization. DO drawdown in bottom waters is fueled by labile organic matter and reduced inorganic materials that are presumably controlled by riverine and non-point sources, and STP discharges. Monitoring programs reveal that discharges from STPs, which include combined sewer overflows (CSOs), supply to LIS an average of 61% of the system's total organic carbon (TOC) loading, totaling ~137,000 tons yr^{-1}, and 73% of total nitrogen nutrient loading, amounting to 53,000 tons yr^{-1}; the remainder deriving from non-point sources (NYSDEC & CTDEP 2000). It is important to consider that STP discharges to LIS are subjected to secondary treatment, a process which reduces biochemical oxygen demand (BOD) by 92% relative to the untreated influent, while only removing ~37% of total nitrogen (NRC 1993). Consequently, BOD in effluents from New York City STPs declined by about 60% during the latter half of the 20th century (O'Shea and Brosnan, 2000). Therefore, labile organic matter directly fueling BOD in the receiving waters today is probably only a small fraction of the reported TOC discharge, most of which may be relatively refractory and slowly remineralized. High precipitation events may promote episodic spikes in BOD because influent from CSOs can temporarily overwhelm STPs, reducing their hydraulic retention times, and cause incompletely treated, high-BOD effluent to enter LIS (Louck and Johnson 1991; St. John et al. 1991). However, over most of hypoxia onset and maturation, marine productivity due to inputs of inorganic nutrients, not TOC, loadings are believed to be the primary driver of oxygen consumption in LIS bottom waters as evidenced in management and modeling efforts (Welsh and Eller, 1991; Welsh 1995). Over timescales of centennia, however, the proportions of autochthonous and allochthonous organic matter have varied considerably, as is clear from core studies (Varekamp et al. 2009a, 2009b, 2010).

The mechanisms by which inorganic nutrients fuel oxygen consumption in bottom waters are indirect and complex. As has been observed in many coastal settings, eutrophication, i.e., excessive macronutrient (N, P, Si) loadings, generally stimulates phytoplankton communities to rapidly proliferate, barring other limitations, such as light exposures, micronutrients or inhibitory chemicals. Several fates are possible for flourishing phytoplankton cells; they can divide, be eaten, lyse after succumbing to viral infection or sink from surface waters. Above the compensation depth during the photoperiod of each day, phytoplankton are net producers of DO, sometimes driving it to supersaturation in surface waters. However, like all aerobes, photosynthetic organisms must also respire continuously. In fact, algal respiration, R_a, in LIS's euphotic zone is estimated to consume 5-52% of gross primary production (GPP) during the day (Goebel et al. 2006). In LIS surface waters, R_a has been estimated to contribute on average 40-50% to total daytime plankton community respiration (R_c) (Anderson and Taylor 2001; Goebel and Kremer 2007). During the night, euphotic zone residents become net sinks for DO, respiring away stored energy reserves. Furthermore, viable phytoplankton residing below the compensation depth for prolonged periods, due to vertical mixing or sinking, continue to respire until energy reserves are totally dissipated. Viable phytoplankton can sink from surface waters as individuals or amorphous aggregates, depending upon species and physiological status (Kiørboe et al. 1996; Lomas and Moran, 2011). Some can also be packaged in metazoan fecal pellets in an undigested state and sink rapidly to depth while presumably still respiring (Dam et al. 1995).

In addition to their own endogenous respiration, phytoplankton fuel respiration of other trophic levels when they: i) fall prey to protistan and metazoan herbivores, ii) release extracellular organic carbon (EOC), iii) decompose, iv) are defecated by herbivores, or v) are lysed by viruses. Heterotrophic prokaryotes (Bacteria and Archaea) and fungi are the beneficiaries of the organic substrates produced by these processes. Vertical export of phytoplankton-derived organic matter to bottom waters through sinking of cells, aggregates, and fecal pellets, through mesozooplankton migrations, and mixing provides a major mechanistic link between inorganic nutrient loadings to surface waters and oxygen consumption in bottom waters (Welsh 1995; Anderson and Taylor, 2001). The efficiency with which inorganic nutrient loadings are translated into bottom water oxygen consumption is dependent upon complex interactions of myriad physical, chemical and biological variables, such as temperature, wind stress, organic matter quality, and plankton community structure (Welsh and Eller, 1991; Vigil 1991; Michaels and Silver 1988; Wilson et al. 2008). While all life stages of fish and invertebrates are important members of the planktonic food webs, their contribution to DO dynamics can largely be ignored. Numerous studies have demonstrated that unicellular organisms dominate R_c, because of their overwhelming abundances and high intrinsic metabolic rates. For example, >98% of planktonic R_c could be attributed to organisms with diameters <30 μm in experimental ~2,500 m^3 coastal mesocosms (Williams 1981). Thus the focus of studies on the genesis of hypoxia has historically been on microorganisms (e.g., Thomas et al. 2000; Gooday et al. 2009).

A previously unpublished study from G. Taylor’s group examined DO dynamics with respect to nutrient inventories, primary production, and bacterial activities at a single site in WLIS (station A4 near Execution Rocks: 40° 52.3'N 73° 44.1'W) through the summers of 1997 and 1998. This study was conducted concurrently with a parallel lower Hudson River Estuary study; station and methodological details for both studies can be found in Taylor et al. (2003a and 2003b). During this study hypoxic bottom waters (<3.0 mg O_2 L^{-1} or <25% sat) were observed only in August of both years with depressed DO concentrations (<5.5 mg O_2 L^{-1} or <67% sat) in the samples immediately preceeding (**Fig.** 53a). Bottom DO rebounded almost completely by mid-October in both years. DO in the mixed layer was near saturation throughout our observations (78-117% sat) and was usually intermediate (59-109 % sat) within the pycnocline. In both years, highest rates of primary production occurred in the weeks prior to and during detection of hypoxia (**Fig.** 53b). Chlorophyll *a* (Chl*a*) inventories within the pycnocline and bottom waters tended to be highest in the spring and decline through summer and fall, paralleling the decline of DO below the mixed layer (**Fig.** 53a, 53b). Within the three layers, heterotrophic bacterial production (BNP), estimated from ^{3}H-thymidine incorporation into DNA and cell sizing measurements, tended to increase through the summer and reach annual maxima when hypoxia was established, then decline into the fall (**Fig.** 53c). In 10 of the 12 observations, the majority of heterotrophic production resided in waters below the mixed layer, similar to Chl*a* distributions. Patterns evident in Figure 53 are consistent with a scenario in which phytoplankton blooms within the mixed layer in spring and early summer are exported to depth passively by sinking or actively via herbivory, where they decompose to fuel microheterotrophic metabolism and thereby draw down bottom water DO in mid to late summer. These analyses also suggest that the euphotic zone (1% of surface irradiance) extended into the pycnocline when waters were relatively clear which appeared to be the case in 5 of our 12 observations. Thus some undefined fraction of primary production and DO production occurred in deeper, stratified waters on these occasions.

Effects of temperature are inherent in the observed seasonal patterns. Firstly, solar insolation warms surface waters from spring through summer to establish physical stratification. Previous studies in western LIS assert that declines in bottom DO may be more dependent upon changes in thermal stratification than changes in point and non-point loadings (Torgersen et al. 1997; O’Shea and Brosnan 2000; Anderson and Taylor 2001; Wilson et al. 2008). This issue is explored in more detail elsewhere in this volume (Wilson et al. this issue). Another important consideration is that water temperature controls DO solubility. In fact, DO concentrations observed in pycnocline and bottom water samples of the study reported here were more strongly correlated with temperature ($r = -0.82$, $p << 0.0001$, $n = 22$) than any other measured variable, explaining 67% of DO's variance. Lastly, rates of chemical reactions and metabolism of poikilotherms vary in direct proportion to water temperature. Bacterioplankton metabolism appears to possess Q_{10} responses lying between 2 and 3, meaning that rates double or triple with a 10°C increase in water temperature (Shiah et al. 2000). Thus, a portion of the seasonal BNP increases observed at station A4 may be driven by warming waters (**Fig.** 53c). In fact, about 40% of the variance ($r = 0.64$; $p < 0.001$, $n = 24$) in bacterial specific growth rates (BNP/bacterial biomass = μ = div d^{-1}) was explained simply by temperature, while the remaining variance is likely explained by labile substrate availability. Because measuring labile substrate availability is impracticable, measurements of ^{14}C-glucose, ^{14}C-glycolate, and ^{14}C-acetate turnover (k, % d^{-1}) were used as proxies for bacterial substrate assimilation activity. Below the mixed layer, turnover of all three substrates were highly correlated with BNP; k_{glu} vs BNP, $r = 0.73$, $p << 0.0001$; k_{gly} vs BNP, $r = 0.61$, $p < 0.05$; k_{ace} vs BNP, $r = 0.86$, $p << 0.0001$. Thus, between 37 and 74% of variance in BNP can be explained by labile substrate turnover. It must be noted that labile substrate turnover probably does not vary totally independently from temperature because processes liberating substrates from biogenic polymers, i.e., enzymatic hydrolysis, are temperature-sensitive (Taylor et al., 2009). Thus covariance among BNP, k_{glu}, k_{gly}, k_{ace}, and temperature is expected.

During this study, water column oxygen consumption was also measured in an automated respirometer within the mixed layer, pycnocline and bottom waters (Taylor et al. 2003a). Community respiration below the mixed layer varied between 0.16 and 4.0 μM O_2 hr^{-1} ($\bar{x}$ = 1.8

μM O_2 hr^{-1}) and on average was 1.4 times slower than in the mixed layer. Rates reported here overlap with those reported by Goebel and Kremer (2007) for direct measurements at 8 LIS stations and depth-dependent trends were similar. However, R_c reported in both these studies are significantly more rapid than those derived from a model developed for a nearby station (E10); 0.12-0.36 μM O_2 h^{-1} (Hyroqual 1995). Using R_c measured in pycnocline and bottom water samples and DO saturation concentrations calculated from temperature and salinity, potential DO turnover rates (k_{Rc}) were estimated (**Fig.** 54). Below the mixed layer at station A4, k_{Rc} varied between 2 and 40% d^{-1}, meaning that if these waters were initially DO-saturated and not ventilated, then planktonic R_c alone would totally deplete DO in 2.5 to 64 days ($\bar{x}$ = 13 d). Clearly, turnover of actual DO inventories in bottom waters was faster at the time of sampling because DO was undersaturated in most instances (**Fig.** 2). Also apparent from this analysis is a requirement for significant physical ventilation from vertical and lateral transport to prevent onset of total anoxia (Torgersen et al. 1997).

Adding estimates of benthic oxygen demand does not significantly alter rates of subsurface DO turnover. To illustrate, the highest published LIS benthic oxygen demand (~47 mmol m^{-2} d^{-1}; Mackin et al. 1991) only contributes 1.5-16.6% to observed total k_{Rc} in bottom waters and averages 6%. Chemical oxygen demand (COD) was previously evaluated in formalin-killed controls and found to be consistently <10% of total R_c (Taylor et al. 2003a). Thus, results from both study years indicate that metabolism of suspended microbial communities usually accounts for >85% of the total oxygen demand below the mixed layer, with benthic communities and COD accounting for the remainder, similar to findings published elsewhere (Welsh and Eller 1991; Anderson and Taylor 2001; Goebel and Kremer 2007). However, sediment communities may periodically account for higher proportions of R_c in the aftermath of seasonal blooms (Aller 1994). The principal sources of nutrients and labile OM, which support R_c, can be episodic and may be associated with rainfall patterns (Anderson and Taylor 2001).

Nitrification is another DO-consuming biological process that is seldom considered in coastal eutrophication and hypoxia studies. It is a chemoautotrophic process transforming ammonium to nitrite then to nitrate, consuming O_2 in both steps and producing biomass from dissolved inorganic carbon (DIC). This process is performed by β- and γ-proteobacteria and ammonia-oxidizing archaea (Francis et al. 2005). Ammonium, the energy donor in nitrification, can be a significant fraction of the total nitrogen in STP effluents. In the lower Hudson River estuary, for example, elevated levels of dark $DI^{14}C$ assimilation (DDA) coincided with high STP-derived ammonium loadings, suggesting that nitrification was locally important in carbon, nitrogen and oxygen dynamics (Taylor et al. 2003a). DDA was measured in surface water samples at station A4 and it strongly covaried with R_c, PO_4^{3-}, total inorganic nitrogen (TIN = $NO_2^- + NO_3^- + NH_4^+$), and EOC produced by phytoplankton (**Table** 1). A portion of DDA may be attributable to anaplerotic reactions of all metabolizing cells. Using the arguments presented in Taylor et al. (2001), observed DDA exceeds maximum predicted anaplerotic CO_2 fixation for phyto- and bacterioplankton combined by as much as 17-fold and averages 3-fold. Thus, excess DDA is plausibly driven by nitrification. All inorganic nitrogen species are summed as TIN here, because their individual distributions with depth and time were extremely coherent. The potential contribution of nitrification to hypoxia, to microbial production entering food webs, and to nitrogen transformations can be cautiously inferred from these results. However, direct measurements using ^{15}N tracers and ancillary molecular approaches (e.g., functional gene/transcript quantification) will be necessary to accurately assess the importance of nitrification in this system.

In the limited data set presented here for station A4, temporal variations in inorganic nutrient (PO_4^{3-}, TIN) explained more variance in R_c than any other metric considered in this study (**Table**s 7 & 8). Variations in inventories of particulate and dissolved organic carbon (POC, DOC), phytoplankton, and bacterioplankton and NPP did not explain observed variance in R_c in either the upper or lower water column. However, bacterial production measurements did covary with R_c in both layers, but only explained ~30% of its variance at best (**Table**s 7 & 8). Correlations between R_c and pheopigments (+) and NPP (-) in pycnocline and bottom water samples are consistent with R_c lagging behind surface productivity and responding to herbivorous activity and delivery of phytodetritus, of which pheopigments are a proxy. However, sampling resolution was far too coarse to resolve potentially lagged responses. Twelve sampling campaigns at a single station are clearly inadequate to fully elucidate the relationships between R_c and a host of controlling variables.

6.7.1.2 Science Gaps and Management Implications

Hypoxia in LIS results from complex interactions among geomorphological, hydrographic, meteorological, allochthonous chemical input, and biological properties of the system. Prolonged stratification and eutrophication appear to be essential ingredients for development of hypoxic bottom waters. Clearly, results presented here and in recent publications support Welsh's (1995) hypothesis that inorganic nutrient loadings to LIS, primarily from municipal STPs, and photosynthetic production fuel the biological respiration that drives the system to hypoxia. Results presented here and elsewhere also support the contention that $\geq$85%

of the oxygen consumption below WLIS's mixed layer is attributable to planktonic microorganisms (bacteria, algae, fungi) with the remainder due to larger planktonic organisms, benthic respiration and chemical oxygen demand. However, the relative contributions to planktonic respiration due to direct remineralization of STP-derived TOC or oxidation of STP-derived ammonium through the nitrification process remain largely unexamined in this system.

As a result of treatment plant upgrades, total inorganic nitrogen loadings from NYC STPs in the 21st century have been significantly lower than they were in the 1980's and 90's (Wilson et al. 2008 and refs therein). Paradoxically, hypoxia has shown no clear indication of abating in duration, intensity nor areal extent in recent years (http://longislandsoundstudy.net/category/status-and-trends/water-quality/). This seeming incongruity suggests that linkages between eutrophication and hypoxia in LIS are not as straightforward as anticipated. For instance, the large amounts of organic matter stored in the sediments represent the system's "memory" and might be remineralized, thus contributing to persistent hypoxia. It is noteworthy that the vast majority of information used to model hypoxia dynamics and develop management strategies is provided by monitoring state variables from which processes are inferred. Better informed management strategies require more experimental observations to develop a thorough mechanistic understanding of the interplay between municipal discharge, physical oceanographic, meteorological and biological variables in promoting hypoxia.

6.7.3 Biological Consequences of hypoxia

6.7.3.1 Effects on Invertebrates

Nutrient induced hypoxia is one the major environmental and management issues in LIS (LISS status and trends 2010). The ecological effects of hypoxia depend largely on its intensity and duration, both of which vary interannually. The bottom waters of western LIS have experienced severe hypoxic episodes for decades, with dramatic changes in ecosystem functioning and declines in ecologically and commercially important species such as shellfish and finfish. Over the past several decades other coastal regions (e.g. Gulf of Mexico, Chesapeake Bay, Baltic Sea) have experienced similar increases in hypoxia and anoxia due to anthropogenic increases in nutrient delivery combined with effects of climate change (Diaz and Rosenberg 2008). There has been a great deal of research on the ecological consequences of this serious and growing problem, much of which has been admirably summarized elsewhere (Breitburg 2002; Breitburg et al. 2009; Conley et al. 2009; Diaz and Rosenberg 1995; Diaz and Rosenberg 2008; Gray et al. 2002; Rabalais et al. 2010; Rabalais and Gilbert 2008; Vaquer-Sunyer and Duarte 2008).

The temporal variation in bottom water oxygen is part of tidal, diurnal and seasonal cycles in estuaries. Wind direction and duration also contribute to variability. Western LIS experiences hypoxia every summer; the severity and duration varies interannually depending on factors controlling mixing and ventilation (Wilson et al. 2008; Kemp et al. 2009). Typically bottom waters in the Narrows and the western basin have dissolved oxygen levels below 3 mg O_2 L^{-1} during July and August. Ecological effects of hypoxia depend strongly on severity and duration, but in most years it has been severe enough in western LIS that the ecological effects have been dramatic and sustained.

All free-living animals require oxygen, but species vary widely in their tolerance to hypoxia. Many coastal benthic species are adapted to survive hypoxic conditions as long as it is not severe hypoxia or anoxia lasting too long. Many species can survive mild hypoxia for over one to two weeks (Diaz and Rosenberg 1995). Differences in tolerance to hypoxia, combined with behavioral and physiological responses to hypoxia and associated stresses characterize interspecific effects and ecological consequences.

Mobile animals such as fish generally move away from hypoxic water. Benthic invertebrates are generally much less mobile than nekton, with the exception of some epifaunal predators (shrimp, mysids, blue crabs). Infauna respond to hypoxic exposure by moving closer to the sediment surface, and under severe hypoxia, will crawl out of the sediment (Diaz and Rosenberg 2008). Sensitivity to hypoxia is typically highest in fish, followed by crustaceans, polychaetes, with bivalves generally being the most tolerant (Gray et al. 2002). At 2 mg O_2 L^{-1}, benthic fauna in the Adriatic Sea exhibited escape responses (with epifauna moving horizontally and infauna moving upward in the sediment); at 0.5 mg O_2 L^{-1}, infauna started to emerge and began to die (Riedel et al. 2008). This behavior is consistent with other studies, and underscores the importance of oxygen concentration on behavior and survival (Diaz and Rosenberg 1995, 2008).

Exposure to periodic hypoxic conditions is common and natural for many coastal benthic organisms, including those living in intertidal zones and in organic rich muds. Inhabitants of these environments exhibit a wide range of physiological adaptations to tolerate hypoxic periods. Animals that cannot escape must either compensate for reduced oxygen to maintain metabolic rate, reduce their metabolic rate, or use anaerobic pathways to process energy (Burnett 1997). Many species respond to moderate hypoxia by increasing ventilation or heart rate to acquire sufficient O_2, but at lower oxygen concentrations, net metabolic rates decline. Some species induce production of respiratory pigments during exposure to hypoxia (Mangum 1997). Many benthic invertebrates that tolerate hypoxia use a variety of anaerobic pathways, with metabolic rates typically reduced under these conditions (Grieshaber et al. 1994). One exception is the transient opportunistic bivalve *Mulinia lateralis*, which maintains high metabolic rate even under anoxic conditions (Shumway et al. 1993). Anaerobic metabolic pathways are crucial mechanisms for tolerating hypoxic episodes, but because animals reduce metabolic rates and do not feed during these periods, growth and secondary production are reduced during severe hypoxia.

Exposure to low oxygen levels in marine environments is typically accompanied by other potential stressors such as sulfide, ammonium, carbon dioxide, and elevated temperature. Marine benthic fauna are invariably exposed to elevated levels of sulfide and ammonium, both of which are toxic to aerobes. Sulfide is the product of anaerobic decomposition of organic matter that uses sulfate as the electron acceptor. Because of the high concentration of sulfate in seawater, bacterial sulfate reduction accounts for a significant fraction of organic matter decomposition in coastal marine muds (Jørgensen 1977). Under hypoxic conditions, sulfide and ammonium build up in sediment pore water and in bottom water because their oxidation is reduced. Many studies that have investigated tolerance to hypoxia have not measured the additive or interactive effects of exposure to elevated concentrations of these toxic compounds (Vaquer-Sunyer and Duarte 2010). Benthic infauna in muds are chronically exposed to micromolar concentrations of porewater sulfide, and most of them exhibit considerable tolerance to it. Benthic invertebrates are able to live in sulfide-rich sediment in part by minimizing exposure through ventilation of overlying water into their tubes and burrows (Aller 1984). They have efficient detoxification mechanisms to oxidize sulfide that is taken up into their tissues, but in most cases these mechanisms require oxygen (Völkel and Grieshaber 1994). Thus under hypoxic conditions they are doubly exposed to the direct stresses of low oxygen level and elevated sulfide exposure. If not all internal sulfide is detoxified, cytochrome c oxidase is inhibited, resulting in sulfide-dependent anaerobic metabolism (Grieshaber and Völkel 1998).

Some species are quite tolerant to sulfide exposure. The enrichment opportunistic polychaete *Capitella teleta* (previously described as *Capitella* sp. I) (Blake et al. 2009) survives and burrows actively at 7 mM sulfide (Wada et al. 2006). Their larvae can survive up to 2 mM sulfide (Dubilier 1988). As described later, *C. teleta* rapidly colonizes organically enriched sediments having high concentrations of porewater sulfide.

Sulfide is toxic to aerobic organisms because it binds to hemoglobin and cytochrome c oxidase (Somero et al. 1989). Some benthic animals may also use sulfide, either through sulfide-oxidizing bacterial symbionts (Fisher 1990; Cavanaugh et al. 2006), feeding on free-living sulfide-oxidizing bacteria (Tsutsumi 1990; Tsutsumi et al. 2001), or even directly as an energy source (Doeller et al. 1999; Parrino et al. 2000; Tielens et al. 2002). But at the high sulfide concentrations found in organically enriched muds of LIS, sulfide is directly toxic causing animals to shift to less efficient anaerobic pathways at higher oxygen levels than they would otherwise. Hypoxic conditions as typically defined (2 mg O_2 L^{-1} or less) are likely to underestimate the combined impact of low oxygen and sulfide exposure (Vaquer-Sunyer and Duarte 2008). Survival during hypoxia is reduced significantly (average 30% higher mortality than hypoxia alone) during sulfide exposure, suggesting that hypoxia effects in natural environments are not due to low oxygen alone (Vaquer-Sunyer and Duarte 2010).

Elevated temperatures reduce survival time and increase the lethal oxygen level (Vaquer-Sunyer and Duarte 2011). Given that the most severe hypoxia occurs in the late summer when water temperatures peak, it is likely that climate change may exacerbate hypoxia-temperature interactions. But in western LIS, warming trend is only exhibited in surface waters above the pycnocline, which are not susceptible to hypoxia (Wilson et al. 2008). The bottom waters of western LIS have trended toward slightly lower summer temperatures because the remnant of the cold pool is isolated by earlier stratification. Thus during most summers, bottom water temperatures may not be exacerbating the effects of exposure to sulfide and ammonium.

Hypoxic bottom waters are also elevated in CO_2 resulting from the mineralization of organic carbon. Even though CO_2 is not toxic in the sense that sulfide and ammonium are, elevated levels can affect organisms in many ways. Elevated concentrations of CO_2 (hypercapnia) produce acidosis in organisms (Burnett 1997). Temperature-induced acidosis has been shown to be deleterious to lobsters (Dove et al. 2005).

6.7.3.2 Effects on Food Webs

Predator-prey interactions are affected in complex ways by hypoxia, depending on its severity and spatial and temporal patterns. During chronic hypoxia, hypoxic water may be a refuge from predators that are less tolerant to low oxygen. For example, chronically hypoxic Narragansett Bay supports a large population of the hard clam *Mercenaria mercenaria* because its main predators, sea stars, fish, and several crab species avoid hypoxic conditions that the hard clam can tolerate (Altieri 2008).

When bottom waters go episodically hypoxic, prey may become more susceptible to predators. In Chesapeake Bay, periods of hypoxia result in higher predation on bivalve *Macoma balthica* because it moves toward the sediment surface , making it more susceptible to predation. Predators move from shallower, more oxic water into recovering hypoxic waters to prey on benthic animals faster than the prey can respond to the recovered conditions by burrowing deeper into the sediment (Long and Seitz 2008). This appears to occur in many cases during periodic hypoxia and recovery (Diaz and Rosenberg 2008).

Even though predators are typically more sensitive to hypoxia, there is considerable variation among species. Lobsters (Howell and Simpson 1994) and blue crabs are relatively tolerant to hypoxia compared to other mobile epibenthic predators, although blue crabs exhibit high individual variability due to differences in hemocyanin structure, possibly due to acclimation history (Bell et al. 2010). Among water column predators, gelatinous animals appear to be more tolerant to hypoxia than fish (Grove and Breitburg 2005). The ctenophore *Mnemiopsis leidyi* uses hypoxic bottom water but its growth and reproduction are reduced at 2.5 mg O_2 L^{-1}. Growth of the scyphomedusan *Chrysaora quinquecirrha* is not affected by hypoxia but it avoids hypoxic water. In general, hypoxic conditions result in more energy flow to bacteria and to gelatinous zooplankton, reducing energy going to higher trophic levels such as finfish.

Early life stages are often more sensitive to hypoxia than adults. Hypoxia can increase mortality of fish embryos. Bay anchovy eggs that sink into hypoxic waters experience higher mortality than those in normoxic conditions (Breitburg et al. 2009) (see Keister et al. 2000).

6.7.3.3 Disturbance, Defaunalization, and Ecological Succession

Severe hypoxia or anoxia result in mass mortality of all exposed animals in the seabed and bottom water. Upon return to more oxic conditions, the sediment is sequentially colonized by a relatively predictable sequence of animals. The model for the ecological succession of the benthos was developed by seminal work in LIS (McCall 1977; Rhoads et al. 1978; Rhoads and Germano 1982, 1986) and in Swedish waters (Pearson and Rosenberg 1978) following both spatial and temporal responses to disturbances including hypoxia, pollution, and dredged sediment disposal. The first group of organisms to colonize sediments defaunated by severe hypoxia are small, tube-dwelling polychaetes, typically spionids and capitellids. These species, characteristically *Capitella teleta* and *Streblospio benedicti* in LIS, have opportunistic life histories characterized by small size, short life span, rapid growth, and high reproductive output. *C. teleta* epitomizes the enrichment opportunist that rapidly colonizes organically enriched muds once oxic conditions in bottom water returns. Sediment porewater has high sulfide concentrations at this stage, making it a geochemically harsh habitat to colonize. But the sediment does not harbor competitors and it is food-rich. *C. teleta* and *S. benedicti* have high tolerances for sulfide (Llanso 1991). Under these conditions food is abundant but oxygen may be limiting, and growth of these colonizers is sensitive to oxygen concentration (Forbes and Lopez 1990). High metabolic potential of these opportunistic species makes them sensitive to oxygen level. *C. teleta* requires high concentrations of labile organic matter to grow. At higher oxygen levels, it has high metabolic rates, independent of the amount of food available, indicating a metabolic system “poised” for aerobic respiration. High population growth rate occurs under conditions of high food and low but increasing oxygen concentrations (Forbes et al. 1994). *C. teleta* can persist in very low population densities (<100 individuals m^{-2}) during unfavorable periods (Tsutsumi 1990). They may survive these periods by shrinking or degrowing (Forbes and Lopez 1990). When conditions become favorable, surviving worms grow rapidly.

The bivalve *Mulinia lateralis* also rapidly colonizes disturbed sediment, and has been known to be a transient opportunist in LIS for over five decades (Sanders 1956; Levinton 1970; Valente et al. 1992). This suspension-feeder exhibits a physiological strategy similar to *C. teleta*, poised for rapid growth under favorable environmental conditions but exhibiting poor survival under environmental stress (Shumway 1983; Shumway et al. 1993). It survives more poorly than many other infaunal bivalves under anoxic and sulfidic conditions. Surprisingly, its metabolic heat dissipation remains high even under anoxic conditions. Its poor ability to regulate metabolism results in poor survival when environmental conditions worsen, such as periods of low food or low oxygen. *M. lateralis* is well-represented in shell death assemblages, but only sporadically in living benthic communities (Levinton 1970).

6.7.3.4 Physiological and Behavioral Responses of Fish

LIS provides numerous productive habitats for the growth of young fish and crustaceans. The bays, harbors, nearshore banks and shallows and their associated wetlands provide a variety of protected nursery areas for early growth and rapid development of important species (Weinstein 1979; McEnroe et al. 1995; Able and Fahey 1998; Smith and Able 2003). Development of hypoxia, through its sublethal and lethal effects on vulnerable early life-stages, degrades effective nursery habitats, diminishing their size and number. Reduction of essential habitats may decrease access to rich-food resources critical to the survival and success of early juvenile populations.

Hypoxia can affect fish directly by altering metabolic rates and their physiological capabilities for tolerance and acclimation, and indirectly through altered behavior that affects abundance and distribution; or through reduced feeding and reduced prey availability (Eby et al. 2005; Pihl et al 1992; Neuenfeldt 2002). Migrations of important anadromous species, including salmon, shad, and sturgeon can be blocked by hypoxic waters (Alabaster et al. 1991; Maes et al. 2007; Weisberg et al. 1996; Albert 1998). Severe hypoxia periodically produces fish kills in LIS. Hypoxia effects on fishes has been the subject of recent reviews (EPA 2000; Richards et al. 2009).

Hypoxia may reduce growth (Bejda et al. 1992; Cech et al. 1984; Stierhoff et al. 2003; Stierhoff et al. 2009a), impair endocrine system function, and disrupt reproduction (Wu et al. 2003; Wu 2002; Landry et al. 2007). Hypoxia is also associated with decreased physical fitness and consequent vulnerability to predation (Roussel 2007), lowered immunity to disease and increased susceptibility to pollutants (Mellergard and Nielsen 1997; Sniesko 1973; Plumb et al. 1976; Walters and Plumb 1980; Lloyd 1961). In consequence, hypoxia acts to decrease fitness, leading to mortalities through decreased abilities to avoid, or tolerate, environmental stressors and to loss of health with vulnerability to predation, disease, and toxicant effects (Health 1987; Pihl et al. 1991; Eby and Crowder 2002; Eby et al. 2005; Taylor and Targett 2007).

A useful summarization of effects of hypoxia on physiology and behavior for LIS fishes is listed on **Table** 9.

6.7.3.4.1 Tolerance

Fishes were the most sensitive marina taxon in an analysis of sublethal and lethal indicators of hypoxia (Vaquer-Sunyer and Duarte 2008). Tolerance to hypoxia for species that occur in LIS has been described by Poucher and Coiro (1997) and Miller et al. (2002) and was reviewed by USEPA in 2000 and 2003 by Breitburg et al. (2003). Early life stages are especially sensitive to low DO (Douderoff and Shumway 1970, Davis 1975, Chapman 1986, Rombough 1988, Breitburg 2002, Miller et al. 2002). In general, lethal oxygen concentrations declined with development from larvae to post-larvae and juveniles. Species mean LC_{50} were greatest for larvae (1.4 -3.3 mg O_2 L^{-1}), intermediate (1.0-2.2 mg O_2 L^{-1}) for post-larvae, and least (0.5-1.6 mg O_2 L^{-1}) for juveniles (Miller et al, 2002) and adults (reviewed in Breitburg et al. 2001; Pihl et al. 1991; Poucher and Coiro 1997; EPA 2000, 2003). Among sensitive early life stages were Bay anchovy eggs 12 hr LC_{50} of 2.7 mg O_2 L^{-1} (Chesney and Houde 1989) and striped bass larvae with a 12 hr LC_{50} of 2.4 mg O_2 L^{-1} (Miller et al 2002).

Many estuarine and marine fishes use nearshore waters and wetlands of LIS as nursery habitats for feeding and rapid growth critical to the success of juveniles (Weinstein 1979; Able and Fahey 1998; McEnroe 1995). Early life-stages of killifishes, silversides, bay anchovy, eels, menhaden, cunner, tautog, sticklebacks, winter flounder, weakfish, bluefish, tomcod and striped bass all inhabit in marshes and creeks that become warm and hypoxic in summer (Talbot and Able 1984; Kimble and Able 2007; McEnroe et al. 1995).

Hypoxia produces a variety of reactions in fish eggs and larvae. It may delay hatching (Voyer and Hennekey 1974), stimulate hatching (DiMichele and Powers 1984), reduce hatching success or induce deformities (Shumway et al. 1964). Hypoxia has slowed larval growth rate, reducing success in development (Rombough 1988), leading to protracted exposure to predators (Giorgi 1981). For species that spawn in deeper water, effects on eggs and larvae will depend on their location in the water column. Striped bass eggs sink below the pycnocline where they are exposed to hypoxia (Keister et al. 2000). Fish larvae have very high specific metabolic rates and high oxygen requirements. Most swimming activity of larvae is supported by aerobic metabolism, as is the capture and digestion of prey. Gills may be absent or poorly developed in early larval stages, so larvae are especially sensitive to periodic as may occur during night-time minima in shallow waters. In many fishes gill filaments become fully functional at metamorphosis, and this is accompanied by production of blood hemoglobin (Da Silver and Tytler 1973). As gills develop oxygen uptake efficiency and hypoxia tolerance increase. For example, in Atlantic herring larvae incipient lethal DO values declined from 3.1 to 2.9 mg O_2 L^{-1} as gills developed, and to 2.2 mg O_2 L^{-1} at metamorphosis; equivalent decline in lethal DO was found for a larval flatfish: 2.7, 2.5, 1.7 mg O_2 L^{-1}, respectively (Da Silver and Tytler 1973).

In general, juvenile and adult fishes had similar ranges of tolerance. For juvenile fish 96 hr LC_{50} ranged from 0.6 -1.6 mg O_2 L^{-1}; for adult fish the LC_{50} range was 0.5-1.6 mg O_2 L^{-1}. Sensitive species with $LC_{50's}$ 1.1 -1.6 mg O_2 L^{-1} include striped bass (*Morone saxatilis*), northern pipefish (*Syngnathus fuscus*), winter flounder (*Pleuronectes americanus*), scup (*Stenotomus chyrsops)*, Atlantic menhaden (*Brevoortia tyrannus)*, and summer flounder (*Paralichthys dentatus*). More tolerant were fourspine stickleback (*Apeltes quadracus*), windowpane flounder (*Scopthalamus aquosus)*, tautog (*Tautoga onitis*), Northern sea robin (*Prionotus carolinus*), hogchocker (*Trinectes maculatus*), and spot (*Leiostomus xanthurus*) with LC_{50} 0.5 - >1.0 mg O_2 L^{-1}(Breitburg et al. 2001; Pihl et al. 1991; Poucher and Coiro 1997; US EPA 2000, 2003).

6.7.3.4.2 Physiological Consequences

A fundamental action of hypoxia on fish is to restrict critical physiological capabilities. Principal physiological effects are directly related to aerobic energetics. Fry (1971) described the relationship of aerobic metabolism to energy production by using the concept of an aerobic metabolic scope for life sustaining activities. Metabolic scope is the aerobic capacity and metabolism that is potentially available for vital activities, including swimming, feeding, growth, etc. Oxygen consumption when quiescent, termed the standard metabolic rate (SMR), is required for physiological maintenance of life processes while fully active oxygen consumption supports the maximum active metabolic rate (AMR). The aerobic scope is the difference between standard and active metabolic rates; it is the metabolism in excess of that required for essential maintenance activities (Fry 1971; Chabot and Claireaux 2008).

In normoxic conditions there is a maximal rate at which any fish can use oxygen. The rate is limited by capacities of the gills and cardiovascular system to take up oxygen and distribute it to the tissues. However, the potential demands for oxygen by all the organs and tissues in aggregate exceed the maximal rate of oxygen uptake (Guderly and Pörtner 2010). The limitation of maximum aerobic capacity of fish causes conflicts among demands of life activities that require aerobic energy, and require partitioning of energy between those demands.

Hypoxia limits the maximal rate of oxygen use in respiration, directly reduces the aerobic scope for vital activities (Brett and Groves 1979). Reviewing the physiological effects of hypoxia on fish, Farrell and Richards (2009) stated that for “all fishes, the zone of environmental hypoxia is characterized by a progressive loss of physiological functions as the hypoxic state deepens and aerobic scope declines”. They suggest that with deepening hypoxia such loss of principal aerobic functions might progress as: first a reduction of locomotion, followed by impairment of reproduction, and later the slowing or cessation of growth. Vaquer-Sunyer and Duarte (2008) reported that there was wide variation in the onset of such sublethal physiological effects among species of fishes; thresholds ranged from 10 to 2 mg O_2 L^{-1}.

Hypoxia occurs in the summer when water temperatures are high, so for ectotherms metabolic rates and oxygen requirements are highest occur when DO levels are lowest. Elevated temperature tends to raise the DO threshold for onset of sublethal effects (Cech et al. 1984; Cech et al. 1990; Schurmann and Steffensen 1992; Schurmann and Steffensen 1997; Secor and Gunderson 1998; Claireaux et al. 2000). As a result, hypoxia tolerance may be severely limited at elevated temperature, and survival may decline rapidly (Schurmann and Steffensen 1997; Shimps et al. 2005; Secor and Gunderson 1998; Campbell and Goodman 2004).

6.7.3.4.2.1 Avoidance

Fishing surveys have reported fish avoidance of hypoxic areas. Avoidance was usually observed as a decline in abundance and horizontal distribution in the catches of several species, accompanied by a decrease in species diversity. Thresholds of DO for such avoidance have commonly been reported in the range of 3-1.5 mg O_2 L^{-1} (Howell and Simpson 1994; Baden et al. 1990; Pihl et al. 1991; Rabalais and Turner 2001; Eby and Crowder 2002). LIS trawl surveys found catches-per-unit-effort were lower in trawl samples taken at < 2 -3 mg O_2 L^{-1}, and at lowest DO concentrations sampled many species were absent (Howell and Simpson 1994). In other estuaries similar avoidance thresholds of 2 -3 mg O_2 L^{-1} have been reported for juvenile menhaden, spot, summer flounder and weakfish (Eby and Crowder 2002; Bell and Eggleston 2005; Tyler and Targett 2007), while Atlantic croaker, hogchocker, and spot appeared to have lower avoidance thresholds, between 1-2 mg O_2 L^{-1} (Bell and Eggleston 2005; Pihl et al. 1991).

In deep waters with chronic hypoxia, fishes moved nearshore to shallower, more oxic waters (Pihl et al. 1991; Breitburg et al. 1992; Eby and Crowder 2002, 2004; Bell and Eggleston

2005). Fishes may show a stronger avoidance response to chronic hypoxia than to episodic hypoxia (Bell and Eggleston 2005).

In laboratory aquaria, estuarine larval and juvenile fishes also move away from hypoxic water. Avoidance thresholds varying greatly among species, from 4 to < 1 mg O_2 L^{-1} (Deubler and Posner 1963; Brietburg 1994; Wannamaker and Rice 2000; Weltzien et al. 1999). Avoidance thresholds are given in **Table** 9. Juvenile Atlantic and shortnose sturgeons avoid water with DO < 3 mg O_2 L^{-1} (Niklitschek 2001; Niklitschek and Secor 2005). Juvenile Atlantic croaker avoid 2 mg O_2 L^{-1} (Wannamaker and Rice 2000). Very low avoidance thresholds at about 1 mg O_2 L^{-1} have been reported for juvenile weakfish, white mullet, and juvenile spot, whereas mummichogs showed little or no avoidance of DO as low as 1 mg O_2 L^{-1} (Stierhoff et al. 2009**;** Wannamaker and Rice 2000). For some species apparent avoidance thresholds reported for the field seem to be higher than those determined in the laboratory (Tyler and Targett 2007; Stierhoff et al. 2009; Brady and Targett 2010), although menhaden had lower avoidance thresholds in the field (Wannamaker and Rice 2000; Eby and Crowder 2002; Schwartz et al. 1981).

6.7.3.4.2.2 Somatic Growth

Hypoxia has been directly associated with reduced growth in fishes, including a number of species commonly inhabiting LIS, and particularly for juvenile stages that inhabit nursery areas of the estuary, including: killifish, Atlantic silversides, striped bass, black sea bass, winter flounder, summer flounder, weakfish, spot and Atlantic sturgeon (Stierhoff et al. 2003; Poucher and Coirio 1997; Cech et al. 1984; Hales and Able 1995; Bejda et al. 1992; Miller et al. 1995; Stierhoff et al. 2006; Stierhoff et al. 2009a, 2009b; McNatt and Rice 2004; Secor and Gunderson 1998). USEPA (2000) made an extensive review of the minimal oxygen levels requirements for growth and survival of estuarine and marine fishes. Among LIS species, larval stages of crustaceans and fishes had higher thresholds for impairment of growth (4.7 mg O_2 L^{-1}) than did older juveniles, 3.3 mg O_2 L^{-1} (Miller et al 1995, Poucher and Coirio 1997). The US EPA advisory criterion for protection of growth in saltwater species, is 4.8 mg O_2 L^{-1} (USEPA, 2000). Here we focus on reports that were made subsequent to the USEPA (2000) review. Thresholds for growth reduction are summarized in **Table** 9.

Under hypoxic conditions, poor feeding occurs in many fishes and has been associated with much of the reduction of growth at low DO (Ripley and Foran 2011, Chabot and Dutil 1999; Stierhoff et al. 2009a and 2009b; Niklitschek 2001). Digestion is an oxidative process that requires increased aerobic metabolism (Brett and Groves 1979), so that hypoxia tends to restrict feeding and slows digestion, thus providing nutrition inadequate for normal growth.

Some fish avoid waters in the DO range associated with inhibition of growth (Breitburg 2002, USEPA, 2000). USEPA review (2000) also reported DO thresholds for fish avoidance behavior. The review concluded that for most species, the DO critical for growth inhibition occurred at approximately the same DO level at which avoidance behavior was reported. That critical DO concentration for growth inhibition was 2 to 3 times greater than the DO for the lethal LC_{50} criterion. More recent studies on juvenile spot, winter flounder, summer flounder, weakfish, and mummichog have found that growth may be impaired at DO concentrations higher than levels inducing avoidance responses (McNatt and Rice 2004; Stierhoff et al. 2006; Stierhoff et al. 2009a, 2009b; Wannamaker and Rice 2000; Stierhoff et al. 2003). Thus, active avoidance might not be sufficient to prevent hypoxia-related growth-impairment.

Growth of striped bass and winter flounder was impacted at relatively high oxygen concentrations close to 5.0 mg O_2 L^{-1} (Cech et al. 1984; Breitburg 1994; Stierhoff et al. 2006).

Growth of summer flounder and Atlantic silversides was impacted at 3-4 mg O_2 L^{-1} (Stierhoff et al. 2006; Poucher and Coirio 1997). Juvenile Atlantic sturgeon growth was depressed three-fold at 3 mg O_2 L $^{-1}$ (Secor and Gunderson 1998) and growth rates of Atlantic and shortnose sturgeons were reduced at 40% saturation (Niklitschek 2001; Secor and Niklitschek 2001, reviewed in US EPA 2003). Juvenile weakfish, Atlantic menhaden, and spot are relatively more tolerant with lower thresholds for growth reduction (DO < 2.0 mg O_2 L^{-1}). Juvenile mummichog were able to maintain growth down to 3.0 mg O_2 L^{-1} without surface access, but with access to the oxygenated water surface at 1.0 mg O_2 L^{-1} they still maintained slow growth as long as they were allowed surface access, but growth declined to 10% of normal levels when surface access was denied (Stierhoff et al. 2003).

At elevated temperatures, growth limitation has been commonly reported to occur at higher DO levels in winter flounder and summer flounder (Stierhoff et al. 2006, 2009; Targett and Miller 2006), spot (McNatt and Rice 2004), and sturgeon (Secor and Gunderson 1998), but not for juvenile weakfish (Stierhoff et al. 2009b).

Many larval and juveniles fishes that inhabit nearshore marshes experience fluctuating diel regimes of oxygen concentration with typical variation from hypoxia during night and in early morning, to hyperoxia during afternoon (Sanger et al. 2002). In laboratory studies, exposure of juvenile winter flounder, summer flounder, and Atlantic menhaden to cycles of oxygen concentration typical of such diel variation reduced growth when the oxygen minima achieved were similar those that lead to decreased growth at constant low DO (Bejda et al. 1992, Steirhoff et al. 2006, McNatt and Rice 2004) and **Table** 9. In episodic hypoxia, growth of juvenile Atlantic croaker was decreased by half (Eby et al. 2005). In contrast, mummichog growth appeared not affected by cycling widely from 1 to 11 mg O_2 L^{-1}, though growth decreased in constant deep hypoxia at 1.0 mg O_2 L^{-1} (Steirhoff et al. 2003).

Summer flounder experiencing conditions of protracted diel hypoxia in the wild had impaired growth at higher oxygen concentrations than those reported for fish exposed to hypoxia in the laboratory (Stierhoff et al. 2006; Stierhoff et al. 2009a). Similar results were found for weakfish: in laboratory studies no growth reduction was found, even at low DO of 2.0 mg O_2 L^{-1} (Stierhoff et al. 2009b), however growth rate of wild-caught fish was apparently impacted by diel fluctuation in oxygen, despite the mean DO rarely dropping below growth protective criteria of 4.8 mg O_2 L^{-1} (Stierhoff et al. 2009a). Reduced growth of fishes in habitats with diel hypoxia has been often been attributed to reduction in habitat area and abundance of prey, leading to increased competition (Eby et al. 2005) or to increased energetic costs of migration (Perez-Dominguez et al. 2006). Juvenile fishes may utilize shallow hypoxic waters because such areas may have fewer piscine predators than adjacent deeper habitats, and may provide shallow refugia for young fish (Paterson and Whitfield 2000; Sogard 1994).

6.7.3.4.2.3 Reproduction

Hypoxia can affect reproductive and endocrine systems profoundly. Wu (2009) reviewed effects of hypoxia on reproduction and development. In adult fish gonadal maturation is a complex aerobic growth process and the maturing gonad is typically one of the largest tissues requiring oxygen. Hypoxia disrupts endocrines associated with reproduction (Wu et al. 2003; Thomas et al. 2007; Cheek et al. 2009; Thomas et al. 2011). Declines occurred in trihydroxy-progesterone, FSH, LH, and GnRH in Atlantic croaker in hypoxia (Thomas et al. 2006; Thomas et al. 2007). Similarly, there was a significant fall in concentrations of plasma sex steroids in hypoxia-exposed *Fundulus heteroclitus* and *F. grandis* (Landry et al. 2007).

Initiation of adult spawning may be delayed or inhibited by hypoxic exposure (Landry et al 2007). One-month exposure to hypoxia (1.7-2.7 mg O_2 L^{-1}) reduced fertility and hatching success in eggs of Atlantic croaker (Thomas et al. 2006; Thomas et al. 2007). Similar findings were reported for Gulf killifish, with females producing fewer eggs (Landry et al. 2007). Recent field studies of killifish and croaker inhabiting marsh creeks with diel hypoxia show characteristics of endocrine disruption and reproductive impairment (decline in gonad size and lower plasma concentration of reproductive hormones) similar to findings from laboratory studies (Cheek et al. 2009; Landry et al. 2007). Thomas and Rahman (2011) reported that in Atlantic croaker collected from chronically hypoxic waters in the Gulf of Mexico, 19% of females had ovarian masculinization and aromatase suppression; these aberrations of normal reproduction, similar to those induced in the lab, suggest that chronic hypoxia causes the disturbances producing masculinization. Further suggestion of the role of hypoxia in masculinization is the greater numbers of males collected from hypoxic waters of the Gulf of Mexico (Shang et al. 2006; Thomas and Rahman 2011). Hypoxia also affects sex differentiation and can even lead to development of a single sex in zebrafish (Shang et al. 2006).

6.7.3.4.2.4 Compensations for Environmental Hypoxia

Fish may be unable to avoid hypoxia. In compensation to hypoxia, fish may enhance oxygen uptake, or decrease oxygen consumption; they often do both. Fishes have developed a variety of morphological, physiological, and behavioral adjustments to improve their abilities to extract oxygen in such impacted environments. However, few such adaptations have been studied for fishes of the Sound.

A specialized behavior of some species is aquatic surface respiration (ASR) in which fish use the surface water, which usually has highest concentrations of oxygen in the water, for gill respiration. Killifishes adopt ASR behaviors with increasing frequency in progressive hypoxia (McEnroe and Allen 1995; Stierhoff et al. 2003). Similar ASR behavior is adopted by other fishes in the Sound (McEnroe, pers. obs.). ASR allows fish to survive and grow in habitats that are otherwise limiting (Weber and Kramer 1983; Stierhoff et al. 2003) but may also expose fish to increased avian predation (Kramer et al. 1983; Kramer 1987; Kersten et al. 1991).

Frequently the most obvious indication that an animal is becoming stressed by low DO is increased ventilation (Pihl et al. 1991; Wannamaker and Rice 2000; Taylor and Miller 2001; Perry et al. 2009; Crocker and Cech 1997). As oxygen becomes increasingly limiting, ventilation rate then declines (Larsson et al. 1976; Perry et al. 2009; McEnroe and Krozlowitz 1996). Oxygen uptake during ventilation is directly related to the surface area of the gill (Hughes 1984). Some fish living in hypoxic water have been reported to possess a greater gill surface area (GSA) than their conspecifics inhabiting normoxic water (Chapman et al. 2000; Chapman and Hulen 2001; Timmermann and Chapman 2004) and in some species GSA can be rapidly altered in response to environmental oxygen (Sollid et al. 2003).

Oxygen uptake also relates to blood hemoglobin (Hb) affinity for oxygen, and the amount of oxygen that can be carried in the blood depends directly on its hemoglobin (Hb) content in the red blood cells (rbc). Under hypoxia, many teleosts elevate blood Hb concentration by increasing the rbc number and thus hematocrit (Hall et al. 1926; Grant and Root 1952; Petersen and Petersen 1990; Stierhoff et al. 2003). Menhaden caught in low DO waters had greater Hb content of blood than did fish caught in normoxic waters (Hall et al. 1926). Windowpane flounder (*Scophthalamus aquosus*) from the hypoxic western LIS had significantly greater volume of red cells (Hct) than flounder from the eastern Sound, possibly in response to exposure to low DO (Dawson 1990). *Fundulus heteroclitus* significantly increased Hct in acute hypoxia (Stierhoff et al. 2003), but Hct declined in chronic hypoxia (Greaney et al. 1980). Some diseases and pollutants may cause increased sensitivity to hypoxia inducing anemia, diminishing red blood cell number, (Calabrese et al. 1975; Dawson 1979; Heath 1987; Mahoney and McNulty 1992), or by damaging gills (Mitchell and Cech 1979).

Hemoglobin in blood of fish living in hypoxic water generally has greater affinity for oxygen, and low P_{50}, when compared with species from normoxic habitats (Campagna and Cech 1981; Weber 1988; Weber and Jensen 1988; Jensen et al. 1993). Hypoxia-tolerant killifish have Hb with very high affinity, followed by monkfish, toadfish, and searobin, (DiMichele and Powers 1984; Powers et al. 1986; Root 1933; Green and Root 1933; Root and Green 1934).

Hypoxia tolerance correlates with both gill surface area and high blood Hb affinity for oxygen (Mandic et al. 2009; Richards 2011) although both these factors are also related to degree of life-style activity (Grey 1954; Hall et al. 1926) and phylogeny (Richards 2011).

6.7.3.4.2.5 Science Gaps and Management Implications

LIS is a large, complex highly productive estuary that sustains significant populations of fishes and harbors important nurseries for fish. Yet LIS is bordered by some of the densest aggregations of people in the US. Inevitably, those vast populations profoundly impacts the ecology of the Sound and its biota through eutrophication and hypoxia. Low oxygen has profound effects on the physiology of fishes, all of them negative. Low DO affects physiology by limiting the aerobic scope available for swimming, feeding, growth, reproduction. As DO concentrations fall, scope is further limited reducing the potential fitness and survival of fishes. Early life stages are especially sensitive to low DO, and hypoxic conditions reduce inhabitability of essential nursery habitats of LIS. USEPA (2000) water quality criterion to protect marine species (4.8 mg O_2 L^{-1}), if achieved throughout LIS, would provide adequate protection for most species inhabiting the Sound. Notwithstanding improvements made, present conditions in the Sound do not meet those criteria most especially during summer. Eutrophication persists.

This short review considers some physiological effects of oxygen depletion. Nevertheless, other physical properties are important, in particular temperature and pH which may act synergistically to exacerbate effects of hypoxia on physiology of fish; they critically reduce capabilities for uptake and transport of oxygen for vital aerobic energetics, fitness and survival. During recent decades temperature and pH have both increased in regional waters. Such changing factors could require future reconsideration of the water quality criteria for DO.

6.7.4 The Biological Invasions of LIS

Introduced species are often prominent members of LIS communities (**Table** 10): at summer's end, a buoy pulled up along the shore may be covered with the Asian green seaweed *Codium fragile fragile* and the Asian sea squirt *Styela clava*, a habitat likely once dominated by the native mussel *Mytilus edulis*. Marina float edges support the Japanese sea anemone *Diadumene lineata* by the millions, a few centimeters above profuse populations of the Asian sea squirt *Botrylloides violaceus*, the European sea squirt *Botryllus schlosseri*, and the Asian sea squirt *Didemnum vexillum*. Along rocky shores, the most common snail is the European periwinkle *Littorina littorea*, and the most common crab is the Asian shore crab *Hemigrapsus sanguineus*. And between 1995 and 2010, new non-native species were detected at the rate of about one new species per year. Nevertheless, the scale and extent – the depth and breadth – of invasions in the Sound have often been lower on the environmental radar: the LIS Study (LISS), in progress since 1985, makes no reference to invasions in their 2010 "Status and Trends in the Health of Long Island Sound" report (LISS 2010).

A question – or comment – typically posed relative to recently glaciated environments such as LIS is whether "everything is really introduced anyway," implying that adding additional species by human-mediated transport simply extends a process already in play. The young age (less than 20,000 years) of, for example, newly deglaciated rocky intertidal shores, and their natural recolonization by characteristic organisms such as barnacles, mussels, crabs, and seaweeds, appears to underscore an "it's invaded anyway" scenario, and that distinguishing *human-mediated activities* from *natural recolonization* is simply a matter of terminology, and not of pattern or process.

Several critical ecological and evolutionary aspects pertain here. Biological invasions consist of two separate and distinct phenomena: *Range expansions* and *introductions*. Range expansions are the movement of species over time by "natural" means, such as current-mediated dispersal of larvae or rafted adults. These movements occur largely along corridors, such as continental margins and island chains, often in response to long-term changes in ocean and shoreline conditions. Introductions are the transport of species by human-mediated vectors (such as shipping), and occur largely across barriers such as ocean basins and continents. These latter events are *sui generis,* having no precedent in Earth history at the time scales involved: we can now move virtually any species anywhere in the world in 24 hours.

Thus, introductions are not simply accelerating natural processes: the vast majority of species involved would not have arrived eventually, simply given enough time (beyond invoking time scales beyond human concern in environmental mediation and management, such as hundreds of millions of years and the movement of continents). Natural recolonization of habitats rendered historically abiotic (by whatever process) typically derives from adjacent donor biotas, and the recolonizing species concerned usually have, in turn, a long evolutionary history in the region (Sorte et al. 2010). In contrast, human-mediated invasions typically bring species from distant regions that lack the longer-term (millennia to millions of years) evolutionary integration and roots of indigenous or endemic taxa. Species brought by ships or other means from European or Pacific theaters are not part of a "natural" continuing post-glacial colonization process, and can (and do) fundamentally change our understanding of the biological, biogeographic, and ecological histories of our shores.

Human-mediated invasions of marine and estuarine organisms into LIS have likely been occurring for nearly 500 years. Giovanni da Verrazano, sailing by LIS in 1524 aboard *La Dauphine* (De Vorsey, 2007), may have been the first European since the Vikings to bring non-native species across the Atlantic to American shores. However, aside from the archeological record (which generally provides a resource for only hard-bodied or hard-shelled organisms), scientific records of the modern-day marine life of LIS date only from the late 1700s and early 1800s, and these early works are fragmentary at best (for example, Herbst 1782-1804; Schoepf 1788; Rafinesque 1817, 1819). A more thorough picture begins to emerge by the late 1800s, but for many groups there are few records until well into the mid-20th century.

A result of these historical lacunae is that many species that may have been introduced between the 1500s and 1800s – a nearly 400 year period! – and that are now common to both

Europe and North America, are assumed, without evidence, to be native naturally-occurring amphiatlantic taxa. These often include well-known ship-fouling species – which attribute alone, however, does not mean that they were introduced. Instead, pending a detailed rendering of their historical biogeography, genetics, biology, and ecology, many taxa now have to be removed from "native" lists and treated as cryptogenic (Carlton 1996), as further discussed below.

As a result of the historiography of LIS biodiversity, our modern understanding of the scale of introductions (and thus their importance in the ecological history) of LIS is highly constrained by our limited knowledge of the early history of invasions. The recent resolution that the common native red alga *Polysiphonia harveyi*, found in 1847 in Stonington, Connecticut is in fact an Asian species (now known as *Neosiphonia harveyi*) introduced on ship hulls (**Table** 10), speaks to our often translucent windows into the past. Our lack of knowledge is not restricted to long-ago eras: our sense of the pulse of changes in biodiversity in the Sound is also limited by the absence of any modern extensive, Sound-wide standard monitoring or observation program. Sometime between the late 1990s and 2010, a large (up to 6 cm in length) shrimp, the Asian *Palaemon macrodactylus*, spread throughout LIS and into Narragansett Bay without notice. Carlton (2009) has reviewed the many additional reasons for the potential underestimation of the number of non-native species. Despite the long-term density of marine biologists from Woods Hole to New York, and despite the recent completion of a decade's global effort focused on censusing marine life, at the beginning of the 21st century, we have no thorough, scholarly atlas of either the historical or modern biota of LIS.

We thus do not know the number of non-native species in LIS. About 70 largely macroscopic non-indigenous species are recognized in the 275 km inland sea corridor from the Hudson River estuary to Buzzards Bay (J. T. Carlton, unpublished). The actual number of non-native species in southern New England may be two or three times that. Examples are presented here (**Table** 10) of some of the more conspicuous and prominent invertebrate invaders, including sea anemones, mollusks, crustaceans, bryozoans, and ascidians. Non-native but largely freshwater fish may enter the brackish or marine waters of the Sound, such as the mosquito fish *Gambusia affinis* and the brown trout *Salmo trutta* (Gordon 1974; Mills et al. 1997; Briggs and Waldman 2002). Certain non-native salt marsh plants are common, such as the introduced genotype of the common reed *Phragmites australis* (Saltonstall 2002). The non-native mute swan *Cygnus olor* is a common omnivore in salt water throughout the Sound (Allin and Husband 2003).

Poorly known are many common and often predominant taxa such as protists, diatoms, foraminiferans, sponges, numerous species of hydroids, nematodes, flatworms, oligochaetes, polychaetes, cheilostome and ctenostome bryozoans, nudibranchs, copepods, amphipods, isopods, and tanaids. Examples of cryptogenic species of some of these groups are shown in **Table** 11. Many of these species are not rare: the hydroid *Obelia dichotoma* (in earlier literature as *O. commissuralis*) has long been a prominent member of regional fouling communities, Nutting (1901) noting it as "abundant in Woods Hole [Cape Cod, Massachusetts] .... growing on piling of wharves and on submerged timbers." The bryozoan *Amathia vidovici* forms prominent fouling masses in LIS in the summer, and have been present in New England since at least the 1850s (Verrill et al. 1873, as a "new species," *Vesicularia dichotoma*). Its biogeographic history remains unknown, as does the history of many other bryozoans.

Most of the recognized invasions of LIS are mollusks, crustaceans, ascidians, and macroalgae, groups that are either larger in size, more tractable taxonomically, or have attracted interest by specialists (such as ascidians and certain common filamentous algae). Approximately half of the non-native species in LIS are European and approximately half have their origin or probable origin in the Pacific Ocean. Of interest is that while nearly three-quarters of the 14 species of non-native algae recognized from southern New England come from the Northwest Pacific Ocean, all of the introduced mollusks (9 species) of clear provenance originate from the Atlantic Ocean: no introduced mollusks from Japan, or the Northwest Pacific in general, are yet established in LIS and adjacent waters (J. T. Carlton, unpublished). The reasons for this contrast remain unknown.

Absent major historical importations of foreign oysters (such as occurred on the Pacific coast of North America and in France), shipping has been the primary vector for non-native species invasions in LIS. Ship-mediated vectors include hull fouling, internally fouled seawater systems (piping and sea chests), ballast water, solid ballast (such as rocks), and the shipworm- and gribble-bored hulls of wooden vessels. Early invasions included a guild of classic European harbor-associated fouling organisms, such as the crab *Carcinus maenas*, and, not shown in **Table** 10, the salt marsh snail *Myosotella myosotis* (present by the 1830s) and the hydroid *Ectopleura dumortieri,* present since about the 1850s (and likely many of the other hydroids in a holding pattern in the cryptogenic bin in **Table** 11). Probably arriving *from* Europe, but possibly not native there, were the sea squirt *Botryllus schlosseri* and the shipworm *Teredo navalis*, both now suspected of originating in the Pacific Ocean. Some of these may be pre-colonial or colonial-era invasions commencing as early as the 1500s and 1600s. Between the 1870s and 1890s, co-incident with a global surge in shipping (Carlton and Cohen 2003; Carlton et al. 2011), the bryozoan *Bugula simplex*, the sea anemone *Diadumene lineata*, and the hydroid *Gonionemus vertens* all first appeared in southern New England.

What followed appears to be a fairly quiescent period of invasions for the next 50 years, marked by apparently few invasions (or by fewer studies). However, starting in the 1950s invasions re-commenced, and in fairly rapid-fire succession prominent fouling organisms began to arrive: the green alga *Codium fragile fragile* in 1957, the sea squirts *Styela clava* (1973), *Botrylloides violaceus* (1974), *Diplosoma listerianum* (1970s), and *Ascidiella aspersa* (1983), and the bryozoan *Bugula neritina* (1985). The 1990s-2000s continued to mark an era of numerous invasions in southern New England, including the bryozoan *Membranipora membranacea* (from earlier inoculations in the Gulf of Maine), the crab *Hemigrapsus sanguineus* (as from earlier inoculations to the south), the alga *Grateloupia turuturu*, the amphipod *Caprella mutica* and the isopods *Ianiropsis* sp. and *Synidotea laevidorsalis*, the sea squirt *Didemnum vexillum*, the shrimp *Palaemon macrodactylus*, the algae *Gracilaria vermiculophylla* and the alga "*Heterosiphonia" japonica*, and others (**Table** 10, and Pederson et al. 2005).

Finally, as Stachowicz et al. (2002) have noted, new invasions of LIS may be mediated by warming waters. These invasions will consist of two guilds: species from overseas that were historically impeded from colonizing New England by previously too-cold temperatures, and species from southern United States waters that are steadily making their way northward (Carlton 2010; Carlton et al. 2011). Harbingers of a future Sound include southern elements that now make only a transient appearance, but may one day overwinter and become part of the established biota. Among these are the bryozoan *Zoobotryon verticillatum*, which can form startlingly large masses (2 meters long by 1 meter wide) fouling marina floats and docks in southern California, and the golf-ball size sea squirt *Styela plicata*, which can become equally prominent. Both have been found sparingly in LIS in the 2000s, as waif populations (*Zoobotryon*) or as individuals (*Styela*). While *Zoobotryon* is unlikely to be native to southern

U.S. waters, and *S. plicata* is native to Asia, future invasions will include native species as well, already reflected in the 1980s establishment of the well-known southern clam *Rangia cuneata* in oligohaline waters of the Hudson River (Carlton, 1992).

6.7.5 Effects of Climate Change on LIS

6.7.5.1 Coastal Acidification in LIS

The combustion of fossil fuels and the resultant increase in atmospheric CO_2 during the past two centuries (I.P.C.C. 2007) has had a multitude of effects on the planet including acidification of the world's oceans. Atmospheric CO_2 levels have increased from preindustrial levels of approximately 280 parts per million (ppm) to 392 ppm today (average for March, 2011 measured at the Mauna Loa Observatory by the Earth Systems Research Laboratory NOAA). The oceans have absorbed nearly one third of the anthropogenically produced CO_2 during the past century (Sabine et al. 2004), altering inorganic carbon chemistry and pH. Model simulations suggest that combustion of the world's fossil fuel supply in the coming centuries could result in a five-fold increase in atmospheric CO_2 levels to nearly 2000 ppm and a decrease in surface ocean pH by 0.77 units (Caldeira and Wickett 2003; Gattuso and Hansson 2011).

The process of fossil fuel combustion promoting increasing concentrations of anthropogenic CO_2 leading to declining levels of pH and CO_3^{2-} in the ocean has generally been referred to as ocean acidification (Doney et al. 2009). While this process impacts all oceanic biota, coastal marine ecosystems, and estuaries are additionally impacted by near-shore-specific processes that can further enhance dissolved CO_2 concentrations. These coastal oceans and estuaries, such as LIS, are shallow ecosystems (< 200 m) where terrestrial, marine, and atmospheric systems interact. Levels of CO_2 in marine environments will continue to rise during this century, but organisms in some coastal zones are already exposed to high levels of CO_2. Many estuaries are ‘net heterotrophic’ due to terrestrial, riverine, and wetland supplements of allochthonous carbon (Gattuso et al. 1998; Ram et al. 2003; Taylor et al. 2003a; Koch and Gobler 2009; Gattuso and Hansson 2012), which can lead to waters that are supersaturated with CO_2. Episodic discharge of acidic river waters into the Gulf of Maine can depress aragonite Ω values with potentially negative consequences for calcifying organisms such as soft-shelled clams (*Mya arenaria*) (Salisbury et al. 2008). Additionally, upwelling can result in coastal waters with CO_2 levels exceeding 1,000 ppm and decreased levels of CO_3^{2-} (Feely et al. 2008; Salisbury et al. 2008; Doney et al. 2009). Moreover, since anthropogenic nutrient loading rates in coastal zones have risen (Howarth 2008), the concomitant increase in the intensity of algal blooms (Beman et al. 2005) and subsequent heterotrophic degradation of bloom-derived organic matter may result in larger declines in pH and increases in CO_2. This may be especially the case in temperate coastal zones, including LIS, during summer when the net heterotrophic nature of these systems can be maximal (Blight et al. 1995; Ram et al. 2003; Thomas et al. 2004). Finally, sediments in estuaries are typically the most heterotrophic part of the system due to the accumulation of sinking organic matter and generally have the highest CO_2 concentrations. The microbial degradation of this organic matter results in the flux of CO_2 at the sediment-water interface (Rasmussen and Jørgensen 1992) and has the same chemical effects as atmospheric fluxes of CO_2, reducing the seawater pH and carbonate ion availability. Estuaries on Long Island and Chesapeake Bay have experienced pCO_2 concentrations between 500-1500 ppm, and pH levels as low as 7.6 (Talmage and Gobler 2009; Waldbusser et al. 2011) suggesting the aforementioned processes are impacting these estuaries and that coastal ocean acidification is already occurring and is likely occurring in LIS. All of this evidence further suggests coastal zones are regions that may regularly experience high levels of CO_2 and may already periodically experience decreased CO_3^{2-} availability.

This decrease in CO_3^{2-} availability may threaten marine organisms with calcifying parts. One group of marine organisms that are affected by increasing CO_2 levels are shellfish (e.g. Miller at al. 2007). Filter-feeding bivalves are considered ecosystem engineers in coastal waters due to the filtration services they provide (Colson and Sturmer 2000, Gutierrez et al. 2003). This filtration has the potential to control eutrophication and harmful algal blooms (Officer et al. 1982; Cerrato et al. 2004), increase light penetration (Newell and Koch 2004), with the latter two processes providing benefit to submerged aquatic vegetation (Carroll et al. 2008; Wall et al. 2008). As such, these organisms can have major effects on ecosystem structure and function (Raillard and Menesguen 1994; Grant 1996; Arnold et al. 2002). Beyond benefits to marine ecosystems, many shellfish are also commercially valuable as a food source (e.g., Cooley and Doney 2009). For example, in 2007, U.S. landings of clams, mussels, oysters, and scallops exceeded $700 million (NMFS 2008) with their ecosystem services as filter feeders far exceeding that value (Costanza et al. 1997).

In recent decades, wild populations of shellfish native to LIS, such as the hard clam or northern quahog, the Eastern oyster, and the bay scallop, *Argopecten irradians*, have been under increasing pressure from overfishing, loss of habitat, hypoxia, and harmful algal blooms, and their populations have experienced precipitous declines (Jackson et al. 2001; Myers et al. 2007). NY estuaries offer prime examples of such declines, as landings from both the hard clam fishery in Great South Bay and the bay scallop fishery in the Peconic Estuary have declined by more than 99% since the early 1980s (NYSDEC 1950-2009). Factors which have been cited as contributing to these precipitous declines include overharvesting (Kraeuter et al. 2008), reduced reproductive success, predation (Kraeuter 2001), harmful algal blooms (Greenfield et al. 2004; Bricelj and MacQuarrie 2007), and a changing food supply (Greenfield et al. 2005; Lonsdale et al. 2007).

Shellfish produce calcareous shells, and the production of these shells depends on the same calcification processes and availability of CO_3^{2-}. Studies of $CaCO_3$ secreting shellfish have found that sediments undersaturated with respect to aragonite (Ω = ~0.3) can cause enhanced mortality of juvenile hard clams (at 0.2 mm, 0.3 mm, 1 mm, and 2 mm size classes) (Green et al. 2004). Coastal ocean acidification is already evident in many estuary settings due to eutrophication, anthropogenic inputs, upwelling, and freshwater inputs (Feely et al. 2008; Salisbury et al. 2008; Waldbusser et al. 2011). Elevated CO_2 concentrations (~740 ppm) have been shown to cause decreased calcification rates in blue mussels (*Mytilus edulis*) and oysters (*Crassostrea gigas*) (a decrease of 25% and 10%, respectively, over present levels; (Gazeau et al. 2007). Berge et al. (2006) described decreased growth and metabolic rates in the blue mussel at pH levels of 7.4. Similarly, in the marine mussel, *Mytilus galloprovincialis*, a reduction in sea-water pH to 7.3 resulted in decreased rates of oxygen consumption, increased nitrogen excretion indicating the net degradation of proteins, and an overall reduction in growth (Michaelidis et al. 2005).

The earliest developmental stages of shellfish, larvae, are critical to the population dynamics of the adult populations, as any decline in larval populations can have profound implications for future shellfisheries (Caley et al. 1996; Gosselin and Qian 1997; Carriker 2001; Cragg 2006; Miller et al. 2009). These earliest developmental stages of calcifying shellfish may also be highly sensitive to increased CO_2 concentrations. Green et al. (2009) demonstrated that increasing surface sediment aragonite saturation state (Ω) from 0.25 to 0.53 can increase the settlement of *Mya arenaria* by three-fold, suggesting that recently settled larvae may be sensitive to CO_3^{2-} availability (Green et al. 2009). Experimentally enhanced CO_2 has been shown to decrease the development rate of Pacific oyster larvae *Crassostrea gigas* (Kurihara et al. 2007) and the mussel, *Mytilus galloprovincialis* (Kurihara et al. 2008). CO_2 can play a central role in influencing the survival and physiology of ecologically valuable bivalve larvae; *Mercenaria mercenaria*, *Crassostrea virginica*, and *Argopecten irradians* displayed dramatic declines in survivorship and delayed metamorphosis under elevated CO_2 concentrations projected for the 21st century and beyond (Talmage and Gobler 2009). *C. virginica* was the most resilient species of the three with lowered growth and survival under elevated CO_2, but only significant decreases in survival under the highest CO_2 treatments (~1500 ppm). *M. mercenaria* and *A. irradians* larvae both displayed increased growth, survival, and more robust and rapid development when grown under pre-industrial (~250 ppm) CO_2 concentrations compared to current levels (~390 ppm) (Talmage and Gobler 2010). Coastal ecosystems already experience elevated levels of CO_2 (Salisbury et al. 2008; Talmage and Gobler 2009; Waldbusser et al. 2011), in part due to decomposition of the large amount of organic matter already present in estuaries (Gattuso et al. 1998; Paerl et al. 1998; Thomas et al. 2004), and bivalve larvae which are spawned into such environments, will experience significant reductions in their survival rates. As our coastal oceans acidify over the next two centuries, there may be selection pressure for bivalves to become more resistant to high CO_2. Acidification of LIS is nearly inevitable, and may already be occurring in areas of increased eutrophication and freshwater inputs.

6.7.6.2 Temperature Affects During Winter and Spring

The winter/spring phytoplankton bloom in LIS (LIS) has historically dominated annual primary production (Riley and Conover 1967). It provides a significant source of organic matter for both pelagic and benthic components of the food web. Timing and magnitude of spring blooms is controlled by several factors, including incident radiation, wind and tidal stress, and water temperature (Iriarte and Purdie 2004).

Temperate coastal systems like LIS typically exhibit a mismatch between the spring bloom and zooplankton grazing because low temperatures restrict zooplankton activity at the time of the bloom (Smetacek 1984; Keller et al. 2001) so that much of the bloom production is deposited ungrazed on the seabed, where this fresh phytodetritus fuels a detritus-based benthic and demersal food web (Graf et al. 1982; Rudnick and Oviatt 1986). Benthic faunal utilization of this material is typically also delayed in temperate systems because of low temperature, and as bottom water warms in spring, microbial and faunal activities rapidly increase (Cheng and Lopez 1991; Gerino et al. 1998).

There is a long term trend of winter warming in the region (Lwiza 2008). Slightly elevated temperatures during the winter/spring dramatically affect the magnitude and fate of the spring bloom (Keller et al. 1999; Keller et al. 2001; Oviatt 2004; Oviatt et al. 2002). In Narragansett Bay, winter conditions ~ 2^{o} C warmer than average ($3\text{-}4^{o}$ C instead of ~$1\text{-}2^{o}$ C) resulted in a weakened phytoplankton bloom caused by higher abundance of grazing planktonic copepods. This slightly warmer water (4^{o}C) allowed copepods to grow fast enough to graze phytoplankton production. Thus slightly warmer temperatures have a major impact on phytoplankton production that is mediated by the response of zooplankton to temperature. Under warmer conditions more production goes to pelagic components of the food web, and less to benthic and demersal components. It is not known whether benthic fauna and sediment microbial communities respond similarly to warming of the water column, but benthic communities definitely respond to decreased input of phytodetritus (Nixon et al. 2009). The long term reduction in the Narragansett Bay winter-spring bloom over the past half century has been caused by warmer winters along with changes in wind mixing and cloud cover. It has resulted in significantly lower input of organic matter to the seabed and reduced benthic metabolism (Nixon et al. 2009; Smith et al. 2010). The region has also experienced reduction in cold water demersal species and increase in warm water pelagic fish. Warmer winter temperature increases predation of the sand shrimp *Crangon septemspinosa* on winter flounder larvae, demonstrating the effect of climate change on predator-prey interactions. Increased in crabs (especially *Cancer* spp.) have also occurred (Collie et al. 2008).

Sensitivity of phytoplankton and zooplankton to meteorological and oceanographic condictions such as slight changes in winter temperature may have ramifications for higher trophic levels and determine relative success, composition, and diet of apex species. The effects of bottom-up control of food webs is complicated by several factors, including species replacement and top-down processes, but a shift in carbon and energy flow through different components of the food web is likely to have great impact on higher trophic level predators such as striped bass, weakfish, and bluefish (Oviatt 2004; Frederiksen et al. 2006, 2007).

The benthos of broad, shallow continental shelves in temperate regions experience a wide annual temperature range; benthos in LIS, for example are subjected to an annual temperature range from ~0 to 22^{o}C. Temperature is likely to control benthic nutrition, especially for detritivores, because it affects both microbial degradation rates and macrofaunal responses. On temperate continental shelves, phytodetritus deposition resulting from the spring bloom often occurs when bottom water temperatures are low, limiting benthic response. Both benthic microorganisms and macrofauna appear to be limited by low temperature during this period (when temperature typically ranges from 0 to 4^{o} C), but they do not respond equally (Hines et al. 1982; Kristensen et al. 1992; Gerino et al. 1997). Graf et al. (1982) showed that microorganisms respond immediately to phytodetritus deposition but most mesothermic benthic macrofauna (an exception is *Macoma balthica*) do not respond until bottom water temperature increases a few degrees. This time lag in macrofaunal response may occur weeks after deposition of the spring bloom. Thus, freshly deposited phytodetritus may be partially mineralized before temperature increases to allow for macrofaunal feeding.

Although colder water species such as *Mytilus edulis* are able to feed at temperatures as low as 1^{o}C (Thompson 1984), many mesothermic macrobenthos typical of LIS do not appear to feed at all at or below ~6^{o}C. The deposit-feeding bivalves *Nucula proxima and Yoldia limatula*, two dominants in central LIS (Gerino et al. 1998), cease feeding at 6^{o} C (Bender and Davis 1984; Cheng and Lopez 1991) and oyster *Crassostrea virginica* stops filtering at ~5^{o}C (Loosanoff 1958; Pomeroy et al. 2006). Bioturbation in temperate regions is controlled by temperature (Gerino et al. 1998; Goedkoop and Johnson 1996; Kristensen et al. 1992); bioturbation by *Neanthes virens* is inconsequential below 6^{o}C.

Heterotrophic microbial activity is also affected by temperature. Temperature changes too often in temperate environments to select for psychrophilic bacteria (Isaksen and Jørgensen 1996; Jørgensen, personal comm.). Nevertheless, mineralization of phytodetritus begins immediately upon deposition, though the rate is sensitive to temperature (e.g. Shiah and Ducklow 1994; Gerino et al. 1998).

The benthos in environments that experience low seasonal variation in temperature (deep sea, polar and tropical regions) exhibit no such time lag between phytodetritus deposition and macrofaunal response; animals respond immediately to fresh food (Stead and Thompson 2003, 2006; Stead et al. 2003; Witte et al. 2003; Hudson et al. 2004; Moodley et al. 2005; McMahon et al. 2006). It is likely that the effect of temperature-controlled time lag in macrofaunal response in temperate regions ramifies through the food web.

6.8 Concluding Remarks

The biological communities of LIS have experienced a wide variety of impacts, including cultural eutrophication, hypoxia, coastal development, introduction of non-native species, and climate change. In some regards the consequences have been dramatic, with strong latitudinal gradients in plankton productivity, changes in critical habitats such as tidal marshes, dramatic declines in important species such as eelgrass, lobster and winter flounder, restructuring of benthos by periodic hypoxia, and the increasing importance of southern nekton species over northern species. In other regards, some aspects have not shown dramatic temporal patterns. There is no evidence that LIS is more eutrophic now than it was 60 years ago.

Our understanding of the biology of LIS is based on decades of research combined with sustained monitoring efforts. Long-term trends have been observed, but they can be obscured by interannual variations. Monitoring of plankton, seagrass, and nekton are sufficiently robust (with some caveats regarding nekton monitoring discussed below) to characterize temporal changes in biomass and community structure at temporal scales ranging from seasonal to multidecadal. Other components of biological community of LIS have been monitored much more sporadically. So little monitoring of the seaweeds is done at present that we might not even know whether important species are in serious decline. Monitoring of benthic animal communities has been infrequent enough to conflate seasonal, interannual, and longer-term trends. Regular monitoring comparing regions experiencing seasonal hypoxia to normoxic regions is also lacking, and shallow water regions are seriously neglected.

We strongly recommend continued and expanded monitoring efforts that cover critical habitats and biological communities in LIS. Plankton (including HAB forming species) and nekton monitoring have been very informative, but without monitoring of the other organisms, it is very difficult to understand or predict how the food web responds to changes. Food web dynamics (biomass, productivity, trophic linkages) are relatively poorly known, with significant gaps in understanding trophic linkages between primary producers and apex predators. It should be possible to take advantage of interannual variations in production and trophic linkages as a kind of natural experiment to better understand the workings of the LIS food web and how it will respond to longer-term changes. For example, we know that much of the long-term trend in warming in LIS is due to warmer winters, and interannual variations in winter minimum temperatures span the range of warming over the past several decades. Slightly warmer winters have been implicated in dramatic changes in phytoplankton production and its fate, yet little is known how these changes ramify through the food web. These natural experiments need to be done at multiple spatial and temporal scales and include multiple habitat types.

The value of monitoring is difficult to overstate but we must be cognizant of its limitations. One of the most important examples of this limitation is the connection between nutrient concentrations and the development of seasonal hypoxia in western LIS. Monitoring has demonstrated the congruence of spatial patterns of nutrients and hypoxia development, but even though nitrogen input in this region has been reduced (with concomitant reduction in chlorophyll concentrations), seasonal hypoxia has not abated. Management strategies have been based on measuring state variables (e.g. O_2, chlorophyll, nutrients) and inferring processes linking them. Experiments and observations are needed to cultivate a better understanding of how several factors are mechanistically linked; these include anthropogenic delivery of nutrients, physical processes controlling stratification and ventilation of bottom water, and the specific biological processes that produce hypoxia. For example, we have a much better understanding of the factors controlling phytoplankton production than we do of its fate. The imbalance between production and mineralization of organic matter in western LIS is poorly understood.

Another example of the limits of interpreting monitoring data comes from the fish surveys. These valuable seasonal surveys have shown long-term changes in relative and absolute abundance of different fish species, with cold water species (dominant in spring) declining and warm water species (dominant in summer and fall) increasing. Nonetheless, the fixed seasonal schedule of these surveys has made interpretation of underlying causes difficult because many of these fish species are highly (and differentially) migratory so their abundance in LIS is highly seasonal.

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Tables

Table 1. Recommended habitat requirements from Chesapeake Bay submerged aquatic vegetation water quality standards compared to recommendations for Long Island Sound (Batiuk et al. 2000; Koch 2001; Yarish et al. 2006; Vaudrey 2008a, 2008b) and to eelgrass restoration site selection parameters for Long Island Sound.

	Chesapeake Bay Guidelines	**Suggested LIS Guidelines**
Primary Requirements		
Minimum Light Requirement (% of surface irradiance)	> 22	> 22
Secondary Requirements		
Chlorophyll *a* (µg/L)	< 15	< 5.5
Dissolved Inorganic Nitrogen (mg/L)	< 0.15	< 0.03
Dissolved Inorganic Phosphorous (mg/L)	< 0.02	< 0.02
Total Suspended Solids (mg/L)	< 15	< 30
Habitat Constraints		
Minimum Depth Limit (m)	Zmin[a] = (MHHW - MLLW) / 2	
Maximum Depth Limit (m)	Zmax[b] = - ln (0.22) / K_d	
Minimum for (Zmax - Zmin)[c] (m)	0.5 m	1 m
Sediment Organic Matter (%)	0.4 to 12	0.4 to 10
Sediment Grain Size	0.4% to 30% fines	< 20% silt and clay
Sediment Sulfide (µM)	< 1000	< 400
Current Velocity (cm/s)	5 < X < 180	5 < X < 100

[a] MHHW refers to mean higher high water, the high tide level during spring tides. MLLW refers to mean lower low water, the low tide level during spring tides.

[b] The value of 0.22 refers to the minimum light requirement of 22% of surface irradiance. K_d refers to the light attenuation coefficient for the waters of concern.

[c] The minimum required difference between the depth of the shallow and deep edge of the bed.

Table 2. Monthly mesozooplankton abundance (ind. m^{-3}) at station H4 (see Fig. 1 for station location). Numbers in parentheses represent the number of months used to calculate a monthly mean. Abundance for 1952-1953 is from Deevey (1956). All other data are from Dam et al. (2010).

Month	**1952-1953 Abundance**	**2002-2004 Abundance**	**2008-2009 Abundance**
January	10530	11459	17010
February	14665	10332 (n=2)	15570
March	35138 (n=2)	15802 (n=2)	32110
April	68650 (n=2)	93556 (n=2)	58120
May	97323 (n=2)	66728 (n=2)	139400
June	142500	82464 (n=2)	204420
July	83840	32332 (n=2)	20350
August	152070	37468 (n=3)	23720
September	80575	21759 (n=3)	
October	19290	8123 (n=3)	12235 (n =2)
November	32735	3363 (n=2)	12830
December	15090	5739 (n=2)	11420

Table 3. Mean annual total mesozooplankton abundance for periods Oct. 2008 - Oct. 2009, March 2007 – Feb. 2008, Aug. 2003 - Aug. 2004, and Aug. 2002 - Aug. 2003. Data from the CT DEEP zooplankton monitoring program (Dam and McManus 2009). See Fig. 1 for station locations.

	Abundance (ind.L^{-1})			
Station	08-09	07-08	03-04	02-03
B3	77.5	61.6	53.6	48.3
D3	41.9	48.6	38.4	34.5
F2	64.8	57.1	39.0	37.5
H4	46.9	55.2	33.2	33.9
I2	49.1	43.6	32.7	30.8
K2	19.4	16.4	11.4	11.1

Table 4. Descriptive statistics for abundance and biomass of ciliate microzooplankton from the CT DEEP monitoring program (August 2002 through October 2009). Data from Dam and McManus (2009).

	Tintinnids No/L	Tintinnid biomass (µgC/L)	Naked ciliates/L	Naked ciliates biomass (µgC/L)	*Mesodinium-like*/L	*Mesodinium-like* biomass (µgC/L)
MAX	5760	1938	8215	122	25671	48
MIN	0	0	0	0	0	0
MEDIAN	40	0	270	1	80	0
MEAN	197.99	6.66	513.76	3.03	418.13	0.94
N	320	320	320	320	320	320
ST DEV	572.14	108.31	794.43	9.17	1629.59	3.12

Table 5. Definitions of the temperature adaptation and depth groups used to classify finfish species captured in Long Island Sound Trawl Survey. Classifications are based on information taken from Collette and Klein-MacPhee (2002) and Murdy et al. (1997).

ADAPTION GROUPS

Adapted to Cold Temperate Waters:

- more abundant north of Cape Cod, MA than south of New York
- behaviorally adapted to cold temperatures, including subfreezing
- preferred temperature range approximately 3-15^{0}C
- spawns at lower end of temperature tolerance

Adapted to Warm Temperate Waters:

- more abundant south of New York than north of Cape Cod, MA
- behaviorally avoids temperatures < 10^{0}C
- preferred temperature range approximately 11-22^{0}C
- spawns at higher end of temperature tolerance

Adapted to Subtropical/Tropical Waters:

- rare north of Chesapeake and occasional or rare in the mid-Atlantic
- strays captured north of mid-Atlantic are usually juveniles
- not tolerant of temperatures < 10^{0}C
- spawns only south of New York Bight

DEPTH GROUPS

Epibenthic (E)

- found exclusively or almost exclusively on the bottom
- feeds almost entirely on benthic prey
- if fished, taken only by bottom gear such as otter trawl nets

Demersal (D)

- associated with the bottom or bottom structure but may use water column occasionally
- feeds primarily on bottom organisms; uses bottom sediments in reproduction
- if fished, taken primarily by bottom tending gear or mid-water gear such as pound nets

Pelagic (P)

- uses the entire water column or primarily surface waters; eggs and larvae develop entirely in surface waters
- feeds primarily on surface prey or a mix of benthic/surface prey
- if fished, taken primarily by off-bottom or surface gear such as drift gill nets or long lines

Table 6. Classification of 95 species of finfish captured in the LIS Trawl Survey by adaptation and depth group. See Table 5 for complete definitions.

Common Name	Scientific Name	Adaptation Group	Depth Group
alewife	*Alosa pseudoharengus*	Cold	P
American plaice	*Hippoglossoides platessoides*	Cold	E
Atlantic Herring	*Clupea harengus*	Cold	P
Atlantic Sturgeon	*Acipenser oxyrinchus*	Cold	D
barndoor skate	*Dipturus laevis*	Cold	E
Atlantic cod	*Gadus morhua*	Cold	D
cunner	*Tautogolabrus adspersus*	Cold	D
fawn cusk-eel	*Lepophidium profundorum*	Cold	E
fourspot flounder	*Hippoglossina oblonga*	Cold	E
goosefish (monkfish)	*Lophius americanus*	Cold	E
grubby	*Myoxocephalus aeneus*	Cold	E
haddock	*Melanogrammus aeglefinus*	Cold	D
little skate	*Leucoraja erinacea*	Cold	E
lumpfish	*Cyclopterus lumpus*	Cold	E
Atlantic mackerel	*Scomber scombrus*	Cold	P
ocean pout	*Zoarces americanus*	Cold	E
northern pipefish	*Syngnathus fuscus*	Cold	E
pollock	*Pollachius virens*	Cold	P
rockling	*Enchelyopus cimbrius*	Cold	E
red hake	*Urophycis chuss*	Cold	E
rock gunnel	*Pholis gunnellus*	Cold	E
rainbow smelt	*Osmerus mordax*	Cold	P
Atlantic salmon	*Salmo salar*	Cold	P
longhorn sculpin	*Myoxocephalus octodecemspinosus*	Cold	E
spiney dogfish	*Squalus acanthias*	Cold	P
searaven	*Hemitripterus americanus*	Cold	E
Atlantic seasnail	*Liparis atlanticus*	Cold	E
Atlantic tomcod	*Microgadus tomcod*	Cold	D
winter flounder	*Pseudopleuronectes americanus*	Cold	E
whiting (silver hake)	*Merluccius bilinearis*	Cold	D
windowpane	*Scophthalmus aquosus*	Cold	E
winter skate	*Leucoraja ocellata*	Cold	E
yellowtail flounder	*Limanda ferruginea*	Cold	E
American shad	*Alosa sapidissima*	Warm	P
Atlantic silversides	*Menidia menidia*	Warm	P
blueback herring	*Alosa aestivalis*	Warm	P
tautog (blackfish)	*Tautoga onitis*	Warm	D
bluefish	*Pomatomus saltatrix*	Warm	P
Atlantic bonito	*Sarda sarda*	Warm	P
black seabass	*Centropristis striata*	Warm	D
butterfish	*Peprilus triacanthus*	Warm	P
clearnose skate	*Raja eglanteria*	Warm	E
conger eel	*Conger oceanicus*	Warm	E
Atlantic croaker	*Micropogonias undulatus*	Warm	D
American eel	*Anguilla rostrata*	Warm	E
gizzard shad	*Dorosoma cepedianum*	Warm	P
hogchoker	*Trinectes maculatus*	Warm	E
hickory shad	*Alosa mediocris*	Warm	P
menhaden	*Brevoortia tyrannus*	Warm	P
northern kingfish	*Menticirrhus saxatilis*	Warm	D
naked goby	*Gobiosoma bosci*	Warm	E
northern searobin	*Prionotus carolinus*	Warm	E
scup (porgy)	*Stenotomus chrysops*	Warm	D
northern puffer	*Sphoeroides maculatus*	Warm	E
striped cusk-eel	*Ophidion marginatum*	Warm	E
lined seahorse	*Hippocampus erectus*	Warm	E
summer flounder	*Paralichthys dentatus*	Warm	E
sea lamprey	*Petromyzon marinus*	Warm	D
smooth dogfish	*Mustelus canis*	Warm	D
smallmouth flounder	*Etropus microstomus*	Warm	E
spotted hake	*Urophycis regia*	Warm	E
spot	*Leiostomus xanthurus*	Warm	D
striped searobin	*Prionotus evolans*	Warm	E
striped bass	*Morone saxatilis*	Warm	P
oyster toadfish	*Opsanus tau*	Warm	E
white pearch	*Morone americana*	Warm	D
weakfish	*Cynoscion regalis*	Warm	D
bigeye scad	*Selar crumenophthalmus*	Sub-Tropical	P
bigeye	*Priacanthus arenatus*	Sub-Tropical	P
crevalle jack	*Caranx hippos*	Sub-Tropical	P
planehead filefish	*Monacanthus hispidus*	Sub-Tropical	P
Lizardfish	*Synodus foetens*	Sub-Tropical	D
lookdown	*Selene vomer*	Sub-Tropical	P
Atlantic moonfish	*Selene setapinnis*	Sub-Tropical	P
northern sennet	*Sphyraena borealis*	Sub-Tropical	P
orange filefish	*Aluterus schoepfi*	Sub-Tropical	P
Atlantic round herring	*Etrumeus teres*	Sub-Tropical	P
roughtail stringray	*Dasyatis centroura*	Sub-Tropical	E
banded rudderfish	*Seriola zonata*	Sub-Tropical	D
rough scad	*Trachurus lathami*	Sub-Tropical	P
sandbar shark	*Carcharhinus plumbeus*	Sub-Tropical	D
sharksucker	*Echeneis naucrates*	Sub-Tropical	P
spanish mackerel	*Scomberomorus maculatus*	Sub-Tropical	P
African pompano	*Alectis ciliaris*	Tropical	P
blue runner	*Caranx crysos*	Tropical	P
dwarf goatfish	*Upeneus parvus*	Tropical	D
glasseye snapper	*Priacanthus cruentatus*	Tropical	D
grey triggerfish	*Balistes capriscus*	Tropical	D
mackerel scad	*Decapterus macarellus*	Tropical	P
red cornetfish	*Fistularia petimba*	Tropical	P
round scad	*Decapterus punctatus*	Tropical	P
red goatfish	*Mullus auratus*	Tropical	D
short bigeye	*Pristigenys alta*	Tropical	P
striped burrfish	*Chilomycterus schoephi*	Tropical	D
yellow jack	*Caranx bartholomaei*	Tropical	P

Table 7. Bivariate Pearson correlation matrix for community respiration (R_c), chlorophyll *a* concentrations (Chl*a*), pheopigments (Pheo), net primary production (NPP), extracellular organic carbon production (EOC), dark DIC assimilation (DDA), bacterial biomass (BBiom), bacterial net production (BNP), ortho-phosphate (PO_4^{3-}), nitrite+nitrate+ammonium (TIN), and particulate and dissolved organic matter (POC, DOC) observed within the mixed layer of station A4. Statistical significance levels are specified as follows: >90%, **>95%** and **>99%**. “ns” = <90% (n = 12 samples).

	Chl*a*	Pheo	NPP	EOC	DDA	BBiom	BNP	PO_4^{3-}	TIN	POC	DOC
R_c	ns	ns	ns	**0.61**	**0.73**	ns	0.56	**0.76**	**0.96**	ns	ns
Chl*a*		ns	ns	ns	ns	**0.78**	ns	ns	ns	**0.87**	ns
Pheo			ns	ns	ns	ns	ns	ns	ns	**0.67**	ns
NPP				ns	ns	ns	ns	ns	ns	ns	ns
EOC					**0.96**	ns	ns	**0.61**	**0.66**	ns	0.54
DDA						ns	ns	**0.74**	**0.78**	ns	0.57
BBiom							0.60	ns	ns	**0.75**	**0.58**
BNP								ns	ns	ns	ns
PO_4^{3-}									**0.84**	ns	ns
TIN										ns	ns
POC											ns

Table 8. Bivariate Pearson correlation matrix for community respiration (R_c), chlorophyll *a* concentrations (Chl*a*), pheopigments (Pheo), surface net primary production (NPP), bacterial biomass (BBiom), bacterial net production (BNP), ortho-phosphate (PO_4^{3-}), nitrite+nitrate+ammonium (TIN), particulate and dissolved organic matter (POC, DOC) and salinity observed below the mixed layer of station A4 unless otherwise noted. Statistical significance levels are specified as follows: >90%, **>95%** and **>99%**. "ns" = <90% (n = 12 pycnocline + 12 bottom water samples).

	Chl*a*	Pheo	NPP	BBiom	BNP	PO_4^{3-}	TIN	N:P	POC	DOC	Salinity
R_c	ns	**0.57**	-0.38	ns	**0.44**	**0.62**	**0.84**	**0.58**	ns	ns	**0.46**
Chl*a*		ns	ns	**0.50**	ns	**-0.46**	**-0.47**	ns	**-0.74**	-0.35	**-0.45**
Pheo			ns	ns	ns	ns	ns	ns	**0.56**	ns	ns
NPP				**0.49**	ns	ns	**-0.42**	**-0.65**	ns	-0.36	ns
BBiom					**0.75**	ns	ns	**-0.49**	**0.41**	ns	**-0.55**
BNP						**0.60**	**0.46**	**-0.52**	ns	ns	**-0.42**
PO_4^{3-}							**0.79**	ns	ns	**0.41**	**0.47**
TIN								**0.68**	ns	**0.48**	**0.55**
N:P									ns	ns	ns
POC										ns	ns
DOC											0.39

Table 9. Effects of low dissolved oxygen on fish physiology and behavior.

Fish Species	**Lab or Field**	**Effects of low dissolved oxygen (DO)**	**Reference**
Teleosts			
Atlantic croaker (*Micropogonias undulates*)	Field	Juvenile croaker present at DO of 1-2 mg O_2 L $^{-1}$, rarely in trawls at DO <1 mg O_2 L $^{-1}$	Bell and Eggleston (2005)
	Field	Chesapeake Bay absent catches < 1.4 mg O_2 L $^{-1}$	Pihl et al. (1991), Eby et al. (2005)
	Lab	Avoid 2.0 mg O_2 L $^{-1}$	Wannamaker and Rice (2000)
	Field	Growth decreased > 50% in habitats with intermittent hypoxia.	Eby et al. (2005)
Atlantic menhaden (*Brevoortia tyrannus*)	Lab	96 hr LC 50 of 1.04 mg O_2 L $^{-1}$	USEPA (2000)
	Lab	1.2 mg O_2 L $^{-1}$ for 24 hr, no mortality, 25 C	Shimps et al. (2005)
	Lab	30-40% mortality at 1.2 mg O_2 L $^{-1}$ for 24 hr, 30 C 100% mortality in < 6hr at 0.6 mg O_2 L $^{-1}$ 100% survival at 1.5 mg O_2 L $^{-1}$ for 2 wks	
	Lab	More tolerant than spot	McNatt and Rice (2004) Shimps et al. (2005)
	Field	Most will avoid 1 and 2 mg O_2 L $^{-1}$	Wannamaker and Rice (2000)
	Field	Avoidance threshold 2.6 mg O_2 L $^{-1}$ threshold Neuse R.	Eby and Crowder (2002)
	Field	Absent Cape fear collections < 1.4 mg O_2 L $^{-1}$	Schwartz et al. (1981)
	Lab	Threshold of avoidance was 2-4 mg O_2 L $^{-1}$	
	Lab	Threshold for growth reduction of 60% DO< 1.5 mg O_2 L $^{-1}$ At 30 ^{o}C; higher growth than at 25^{o}C, reduced 63% at 1.5 mg O_2 L $^{-1}$ and 25^{o}C.	Wannamaker and Rice (2000)

			Wannamaker and Rice (2000)
Atlantic silversides *(Menidia menidia*)	Lab	Growth decreased 47% after 28 d at 3.9 mg O_2 L^{-1}	Poucher and Coirio (1997)
Inland silversides *(Menidia beryllinia*)	Lab	96 hr LC_{50} of 1.4 mg O_2 L^{-1}	Miller et al. (2002)
Bay anchovy (*Anchoa mitchilli*)	Field Field	Present at 1.5 mg O_2 L^{-1} 96 hr LC_{50} 1.6 mg O_2 L^{-1} for larvae Bay anchovy stay in well-oxygenated surface waters, make brief forays to hypoxic bottom water to feed.	Robinette (1983) Chesney and Houde (1989) Ludsin et al. (2009)
Bluefish *(Pomatomus saltatrix)*	Field Field	Avoided < 4 mg O_2 L^{-1} Absent NY Bight when low DO	Middaugh et al. (1981) Oliver et al. (1989)
Hogchocker *(Trinectes maculatus)*	Lab Lab Lab Field	24 hr LC_{50}=0.5 mg O_2 L^{-1} Survive 1.0 mg O_2 L^{-1} for 10 d Die within 1 d at 0.4 mg O_2 L^{-1} Chesapeake present in trawls at low DO <1.4 mg O_2 L^{-1}	Pihl et al. (1991)
Inland Silversides *(Menidia beryllina)*	Lab Lab	96 hr LC_{50} = 1.0 mg O_2 L^{-1} 24 hr LC_{50} = 1.4 mg O_2 L^{-1}	USA EPA (2000) Miller et al. (2002)

Mummichog (*Fundulus heteroclitus*)	Lab	Juveniles no mortality 9d at 1.0 mg O_2 L $^{-1}$ at 25 ^{o}C	Stierhoff et al. (2003).
	Lab	Maintained growth to 3.0 mg O_2 L $^{-1}$;	Stierhoff et al. (2003).
	Lab	Growth decreased 60% at 1.0 mg O_2 L $^{-1}$ with surface access; reduced 90% w/o surface access.	Stierhoff et al. (2003).
	Lab	No effect of diel hypoxia 1-11mg O_2 L $^{-1}$	Stierhoff et al. (2003)
	Lab	No avoidance of 1 vs 4 mg O_2 L $^{-1}$	Wannamaker and Rice (2000)
Red drum (*Sciaenops ocellatus)*	Lab	Larval 96 hr LC $_{50}$ = 1.8 mg O_2 L $^{-1}$	Miller et al. (2002)
Spot *(Leiostomus xanthurus)*	Lab	24 hr LC$_{50}$ values of 0.7 mg O_2 L $^{-1}$	USEPA (2000)
	Lab	1.2 mg O_2 L $^{-1}$ for 24 hr, no mortality, 25 ^{o}C	Shimps et al. (2005)
	Lab	30-40% mortality at 1.2 mg O_2 L $^{-1}$ and 30 ^{o}C for 24 hr	
	Lab	100% mortality in < 6hr at 0.6 mg O_2 L $^{-1}$	
	Lab	Juveniles low avoidance threshold of $\leq$1.0 mg O_2 L $^{-1}$	Wannamaker and Rice (2000)
	Field	No negative trend in abundance with DO	Bell and Eggleston (2005)
	Field	Chesapeake present in trawls at low DO <1.4 mg O_2 L $^{-1}$	Pihl et al. (1991)
	Field	Move into hypoxic waters	Pihl et al. (1992)
	Lab	Growth reduced 31% at 25C and 89% at 30 ^{o}C after 14d at DO$\leq$1.5 mg O_2 L $^{-1}$	McNatt and Rice, (2004)

Striped bass (*Morone saxatilis*)	Lab	Reduced growth of juveniles in hypoxia (4.7-5.3 mg O_2 L^{-1}) compared to normoxia (6.8-8.2 mg O_2 L^{-1}) at 15 and 20 ^{o}C	Cech et al. (1984)
		DO $\leq$4.0 -5.3 mg O_2 L^{-1} reduced growth	Woods et al. (1985), Lewis and Heidinger (1981), Brandt et al. (1998) (reviewed in USEPA 2003)
		O $\leq$4.0 mg O_2 L^{-1} reduced growth of juveniles	
	Field	$\leq$3.0-4.0 mg O_2 L^{-1} reduced feeding in fish 2 and 4 yrs old	Breitburg (1994), Kramer (1987)
		$\leq$3.0 mg O_2 L^{-1} reduced swimming, agitated	Chittenden (1971)
			Breitburg et al. (1994)
Summer flounder (*Paralichthyes dentatus*)	Lab	24 hr LC_{50} = 1.59 mg O_2 L^{-1} for juveniles at 24-25 ^{o}C	USEPA (2000)
	Field	Absent in trawls DO< 2 , decline in abundance between DO 2-4 mg O_2 L^{-1}	Bell and Eggleston (2005)
	Lab	Growth of juveniles reduced 25% at $\leq$3.5 mg O_2 L^{-1} and 50-60% at 2.0 mg O_2 L^{-1} at 20 & 25 ^{o}C for 14 d	Stierhoff, Target and Miller (2006)
	Lab	Reduced growth in diel cycling (2-11 mg O_2 L^{-1}) regime	Stierhoff, Target and Miller (2006)
		At $\geq$ 25 ^{o}C growth was reduced at 5.0 mg O_2 L^{-1}, At 30 ^{o}C, 90% reduction in growth at 2.0 mg O_2 L^{-1}	Stierhoff, Target and Miller (2006)
	Field	Reduced growth rates in fish in creek with DO cycle of 0.1-17 mg O_2 L^{-1}; significantly reduced growth between 3.5-5.0 mg O_2 L^{-1}	Stierhoff, Target and Miller (2006)
		Growth rate decrease in wild-caught fish after $\geq$120 d with	

	Field	mean DO rarely dropping below growth protective criteria of 4.80 mg O_2 L^{-1}, temperatures 16-32 ^oC	Stierhoff, Targett and Power (2009)
Weakfish (*Cynoscion regalis*)	Lab	Avoidance threshold of 1 mg O_2 L^{-1}	Steirhoff et al. (2009b)
	Lab	Growth unaffected by constant DO of 2.0 mg O_2 L^{-1} for 7 d, nor by diel cycling hypoxia of 2-11 mg O_2 L^{-1} at 20, 25 and 30 ^oC	Stierhoff, Tyler and Target (2009b)
	Field	Growth rate decrease in wild-caught juvenile fish mean DO rarely dropping below growth protective criteria of 4.80 mg O_2 L^{-1}, temperatures 16-32 ^oC for > 120d.	Stierhoff, Targett and Power (2009)
	Field	Juvenile weakfish leave when DO< 2 mg O_2 L^{-1} and quickly return when DO rises > 2 mg O_2 L^{-1}	Tyler and Targett (2007)
	Lab	Reduced activity at DO< 2.8 mg O_2 L^{-1}; prior exposure to hypoxia altered swimming behavior.	Brady, Targett & Tuzzolino (2009)
Winter flounder (*Pleuronectes americanus*)	Lab	24 hr LC_{50} value of 1.4 mg O_2 L^{-1}	USEPA (2000)
	Lab	At 20C juvenile growth reduced 50 and 60% at 5.0 and 3.5 mg O_2 L^{-1}; growth zero at 2.0 mg O_2 L^{-1}. At 25 C poor growth at all DO levels, lost weight at 2.0 mg O_2 L^{-1}.	Stierhoff, Target and Miller (2006)
	Lab	Significant growth reduction in juveniles at 2.2 mg O_2 L^{-1}.	Bejda et al. (1992)
	Field	Growth depression of juveniles occurred at a mean DO of 5.0 mg O_2 L^{-1} after 49d growth in field.	Stierhoff, Target, and Miller (2009)
	Field	Juvenile growth declined in relation to time spent at DO $\leq$ 2.3 mg O_2 L^{-1} in Narragansett Bay.	Meng et al. (2008)
	Lab	P_{crit} juveniles > 3.8 but < 4.3 mg O_2 L^{-1} at 20 ^{o} C	Voyer and Morrison 1971
Chondrosteans			
Atlantic sturgeon *(Acipenser oxyrinchus)*	Lab	High mortality of YOY at 3 mg O_2 L^{-1} for 10 d at 26 □C	Secor and Gunderson (1998)
	Lab	Juveniles Avoid DO < 3 mg O_2 L^{-1}	

	Lab	Juveniles exhibited 3-fold decrease in growth in hypoxia (3 mg O_2 L^{-1}) vs normoxia (7 mg O_2 L^{-1}) at 26° C	Niklitschek (2001), Niklitschek and Secor (2005)
	Lab	Juveniles decreased growth at 40% oxygen saturation at 20 and 27 °C, approximately 3.3 and 2.9 mg O_2 L^{-1}, respectively	Secor and Gunderson (1998)
	Lab		Niklitschek (2001), Secor and Niklitschek (2001)
Shortnose sturgeon (*A. brevirostrum*)	Lab	24 hr LC_{50} values of 2.7 and 2.2 mg O_2 L^{-1} at 77and 104 days post-hatch (dph) at 20 °C, which rose to 3.1 mg O_2 L^{-1} at 27 °C	Campbell and Goodman (2004)
	Lab	Juveniles avoid DO < 3 mg O_2 L^{-1}	Niklitschek (2001), Niklitschek and Secor (2005)
	Lab	Decreased growth of juveniles at 40% oxygen saturation at 20 & 27 °C, approximately 3.3 and 2.9 mg O_2 L^{-1}, respectively	Niklitschek (2001) Secor and Niklitschek (2001)

Table 10. Examples of Marine and Estuarine Invasions from Long Island Sound.

First occurrence is a date of first report or the date of first collection but not necessarily the date of *introduction*. A given species may have been collected earlier elsewhere on the Atlantic coast.

Origins:		*Vectors*:			
NWP	Northwest Pacific Ocean	SB	Ship boring	BR	Ballast Rocks
SP	South Pacific Ocean	SF	Ship fouling	BW	Ballast water
WP	Western Pacific Ocean	IR	Intentional release		

Taxon / Species	Origin	First Occurrence in Southern New England / New York	Vector (to Atlantic North America)	Remarks	Reference(s) documenting or reviewing first discovery or other occurrences in southern New England
CNIDARIA **Anthozoa**					
Diadumene lineata (= *Haliplanella luciae*) (Orange-striped sea anemone)	NWP	1892	SF	A clonal species that can achieve extraordinary abundance in fouling on floats.	Verrill, 1898
MOLLUSCA **Gastropoda**					
Littorina littorea (European common periwinkle)	Europe	1875	BR / IR	Abundant on rocky intertidal shores, mud-sand flats, pilings, and salt marsh edges.	Carlton, 1982; Blakeslee et al., 2008
Bivalvia					
Teredo navalis (shipworm)	SP?	<1860s	SB		Carlton, 1992
CRUSTACEA **Isopoda**					
Ianiropsis sp.	NWP?	1999	SF / BW	A tiny, abundant isopod in fouling communities.	Pederson et al., 2005
Amphipoda					
Caprella mutica	NWP	1998	SF / BW	Now most abundant caprellid in Long Island Sound fouling communities.	Boos et al., 2011
Microdeutopus gryllotalpa	Europe	1871	SF		Myers, 1969; Bousfield, 1973

Decapoda **Brachyura**					
Carcinus maenas (European shore crab)	Europe	<1817	SF / BR	Say (1817) reported this crab based upon a specimen collected by then 17-year old Titian Peale, later a well-known American naturalist and artist. Less common intertidally since the arrival of *Hemigrapsus* in the 1990s.	Carlton and Cohen, 2003
Hemigrapsus sanguineus (Asian shore crab)	NWP	1992	BW	Abundant in rocky intertidal; also in salt marshes and subtidal fouling communities.	McDermott, 1998
Caridea					
Palaemon macrodactylus (Oriental shrimp)	NWP	2001	BW	Common in brackish water fouling communities.	Warkentine and Rachlin, 2010
BRYOZOA **Cheilostomata**					
Membranipora membranacea	Europe	1990	BW	Common on kelp blades.	Berman et al., 1992
Bugula neritina	SP?	1985	SF	Appearing in New England as permanently established populations in the 1980s. Very abundant in summer fouling communities.	McGovern and Hellberg, 2003
Bugula simplex	Mediterranean	1871	SF	In pre-1960s New England literature as *Bugula flabellata*, a distinct European species not in North America.	Ryland and Hayward, 1991; Ryland et al., 2011
KAMPTOZOA					
Barentsia benedeni	Europe	1977	SF	No doubt present much earlier than the first records reflect, and much more widely distributed. Forms dense fouling mats in brackish water.	Canning and Carlton, 2000
CHORDATA **Ascidiacea**					

Botryllus schlosseri	Europe (WP?)	1838	SF	"This is the most handsome and conspicuous compound ascidian found on the eastern coast of the United States" (Van Name, 1945). Abundant in fouling communities.	Verrill et al., 1873
Botrylloides violaceus	NWP	1974	SF		Whitlatch and Osman, 2000; Pederson et al., 2005
Styela clava	NWP	1973	SF	Often very abundant in fouling communities; reaching 15 cm and more in height.	Whitlatch and Osman, 2000; Pederson et al., 2005
Styela canopus (= *S. partita*)	NWP	*Circa* 1870	SF	In the 1800s and early 1900s *S. canopus* was described as occurring "in summer in large masses on the piles of wharves" (Van Name, 1912) in southern New England, along with the native ascidians *Aplidium constellatum* and *Perophora viridis* and the cryptogenic ascidian *Didemnum candidum* [as *D. lutarium*]; both *S. canopus* and *D. candidum* have become rare since the arrival during and since the 1970s of *Styela clava, Ascidiella aspersa, Botrylloides violaceus*, and other new fouling organisms.	Pederson et al., 2005
Ascidiella aspersa	Europe	*Circa* 1983	SF	Common in fouling communities.	Whitlatch and Osman, 2000; Pederson et al., 2005
Diplosoma listerianum	NWP? (widely stated as Europe)	1970s	SF	Common in fouling communities.	Whitlatch and Osman, 2000; Pederson et al., 2005
Didemnum vexillum	NWP	2000	SF	Often abundant in fouling assemblages, and one of the few non-native species found in the open ocean, now occurring in abundance on Georges Bank.	Kott, 2004; Pederson et al., 2005; Lambert, 2009

ALGAE

Chlorophyta (green algae)					
Codium fragile fragile (= *Codium fragile tomentosoides*)	NWP	1957	SF (not commercial oysters)	Abundant in sublittoral and common in low intertidal.	Carlton and Scanlon, 1985; Mathieson et al., 2008a, 2008b
Rhodophyta (red algae)					
Grateloupia turuturu (= *G. doryphora*)	NWP	1996	SF	First detected in Narragansett Bay, and now becoming more common in Long Island Sound.	Marston and Villalard-Bohnsack, 2002; Mathieson et al., 2008a, 2008b, 2008c
Antithamnion hubbsii (= *A. pectinatum* auctt.*;* = *A. nipponicum*)	NWP	1986	SF / BW	Often abundant intertidally.	Marston and Villalard-Bohnsack, 2002
Dumontia contorta (= *D. incrassata*)	Europe	1928	SF		Mathieson et al., 2008b
"Heterosiphonia" japonica	NWP	2009	SF / BW	Thousands of specimens washed ashore in Rhode Island after Hurricane Bill, signaling the presence of this species on the Atlantic coast.	Schneider, 2010
Bonnemaisonia hamifera (= *Asparagopsis hamifera; = Trailliella intricata)*	NWP	1927	SF		Mathieson et al., 2008a, 2008b
Neosiphonia harveyi (= *Polysiphonia harveyi*)	NWP	1847	SF	Common intertidally.	McIvor et al. 2001; Mathieson et al., 2008a, 2008b
Lomentaria clavellosa	Europe	1971	SF		Mathieson et al., 2008a, 2008b

Table 11. Cryptogenics: Examples of species in Long Island Sound that may be native or introduced.

- Porifera
  - *Halichondria bowerbanki*
  - *Haliclona canaliculata*
  - *Leucosolenia* sp.
  - *Lissodendoryx isodictyalis*
  - *Scypha* sp.

- Hydrozoa (hydroids)
  - *Amphinema dinema*
  - *Amphinema rugosum*
  - *Campanularia hincksii*
  - *Clytia hemisphaerica*
  - *Dynamena pumila*
  - *Ectopleura larynx*
  - *Ectopleura crocea*
  - *Gonothyraea loveni*
  - *Halecium halecinum*
  - *Laomedea calceolifera*
  - *Obelia dichotoma*
  - *Obelia bidentata*

  - *Opercularella lacerata*

  - *Pennaria disticha*
  - *Plumularia setacea*

  - *Protohydra leuckartii*
  - *Sarsia tubulosa*

- Polychaeta
  - *Arabella iricolor*
  - *Autolytus prolifer*
  - *Brania clavata*
  - *Eumida sanguinea*
  - *Fabricia sabella*
  - *Harmothoe imbricata*
  - *Lepidonotus squamatus*
  - *Loimia medusa*
  - *Myxicola infundibulum*
  - *Nicolea zostericola*
  - *Phyllodoce maculata*

- Bryozoa
  - *Electra* spp.
  - *Conopeum* spp.
  - *Cryptosula pallasiana*
  - *Bowerbankia* spp.
  - *Amathia vidovici*
  - *Anguinella palmata*
- Amphipoda
  - *Caprella penantis*
  - *Caprella equilibra*
- Tanaidacea
  - *Leptochelia savignyi*
  - *Tanais dulongii*
- Ascidiacea
  - *Ciona intestinalis*
  - *Didemnum candidum*
  - *Perophora viridis*

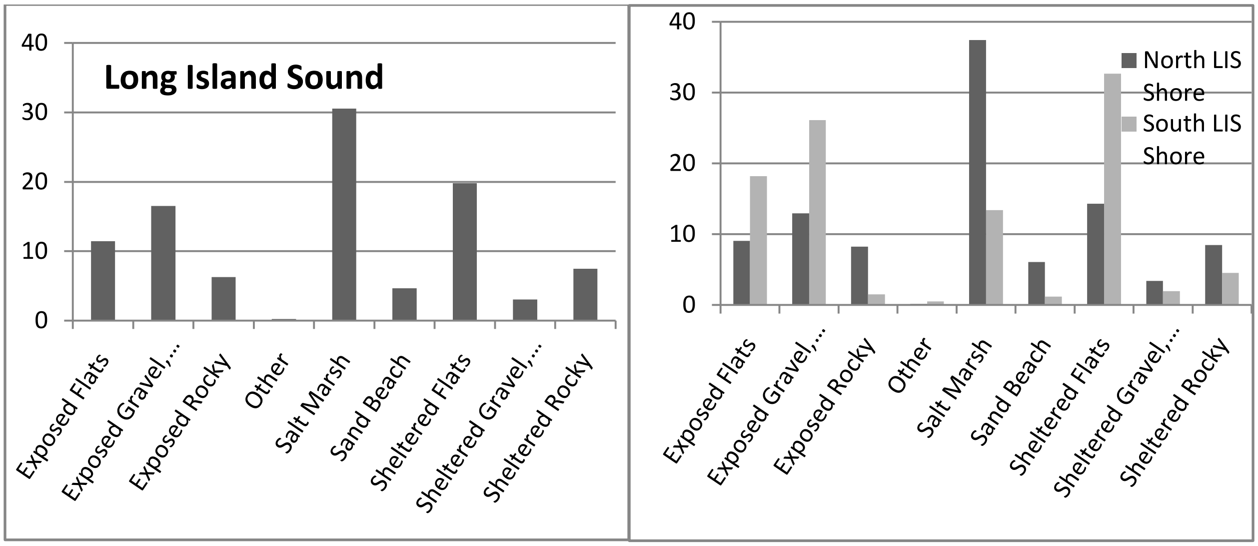


Figure 1. Distribution of intertidal habitats bordering Long Island Sound. Data were derived from Environmental Sensitivity Index (ESI) GIS maps obtained from the NOAA Office of Response and Restoration (http://response.rerstoration.noaa.gov/esi). For each segment of coastline, the most shoreward ESI class was retained, and multiple ESI classes were grouped to simplify the classification.

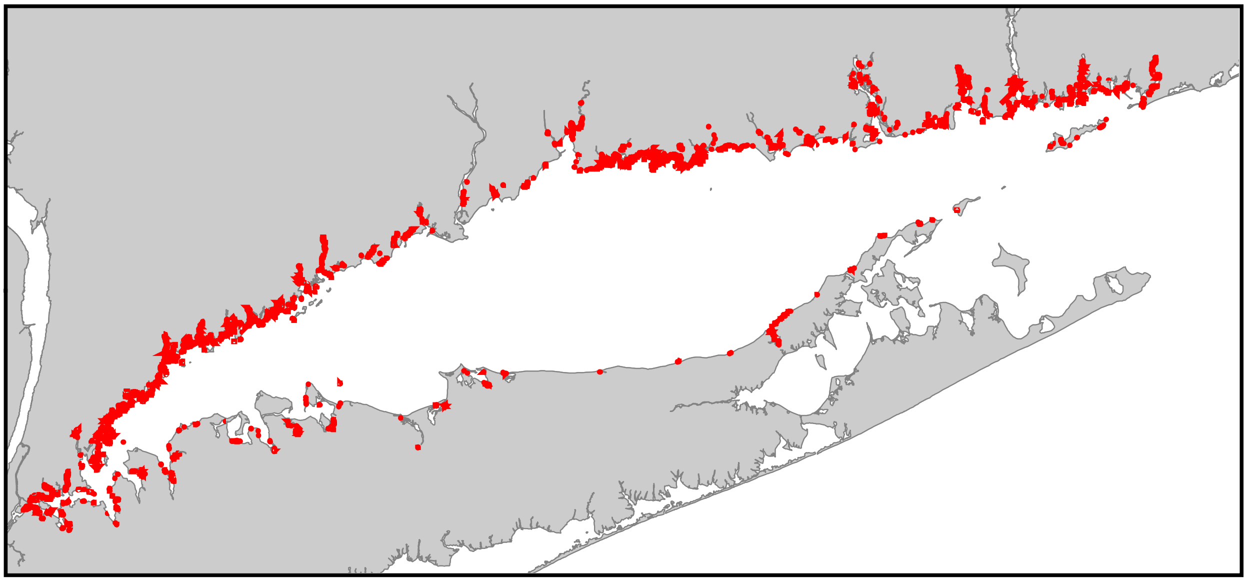


Figure 2. Distribution of rocky intertidal habitats. Data were derived from Environmental Sensitivity Index GIS maps obtained from the NOAA Office of Response and Restoration (http://response.rerstoration.noaa.gov/esi).

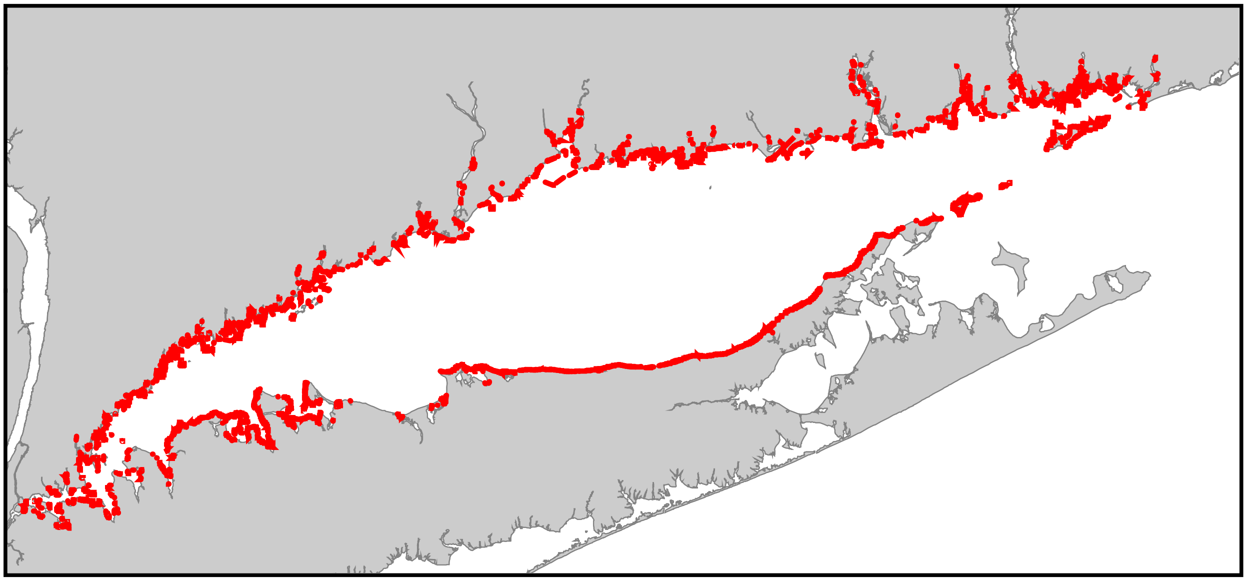


Figure 3. Distribution of gravel, cobble, and riprap. Data were derived from Environmental Sensitivity Index GIS maps obtained from the NOAA Office of Response and Restoration (http://response.rerstoration.noaa.gov/esi).

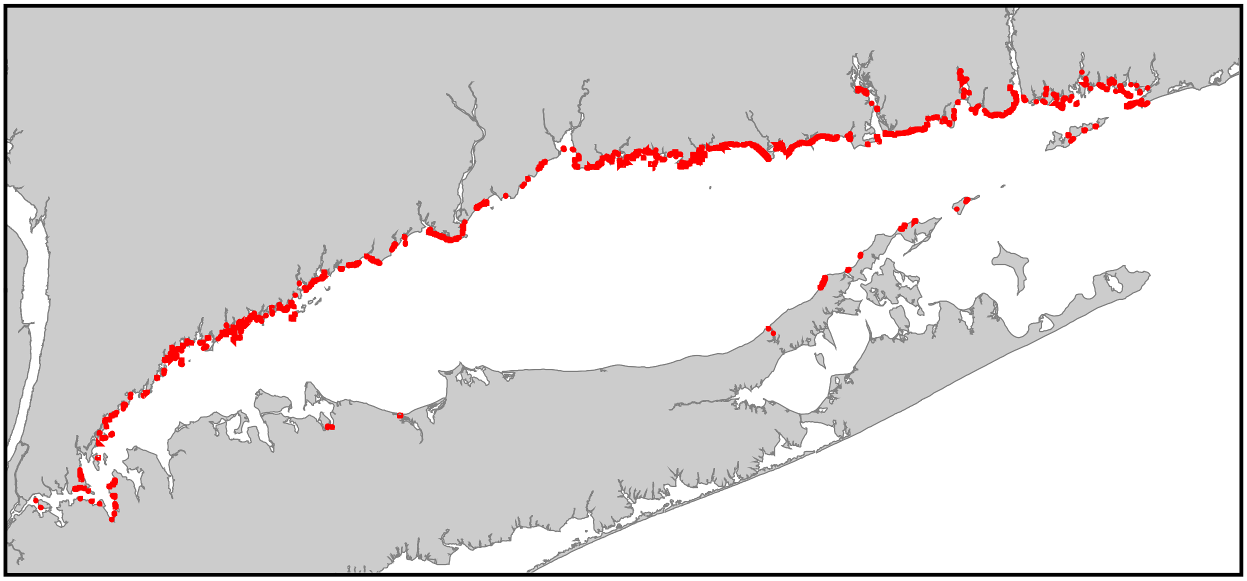


Figure 4. Distribution of sand beaches. Data were derived from Environmental Sensitivity Index GIS maps obtained from the NOAA Office of Response and Restoration (http://response.rerstoration.noaa.gov/esi).

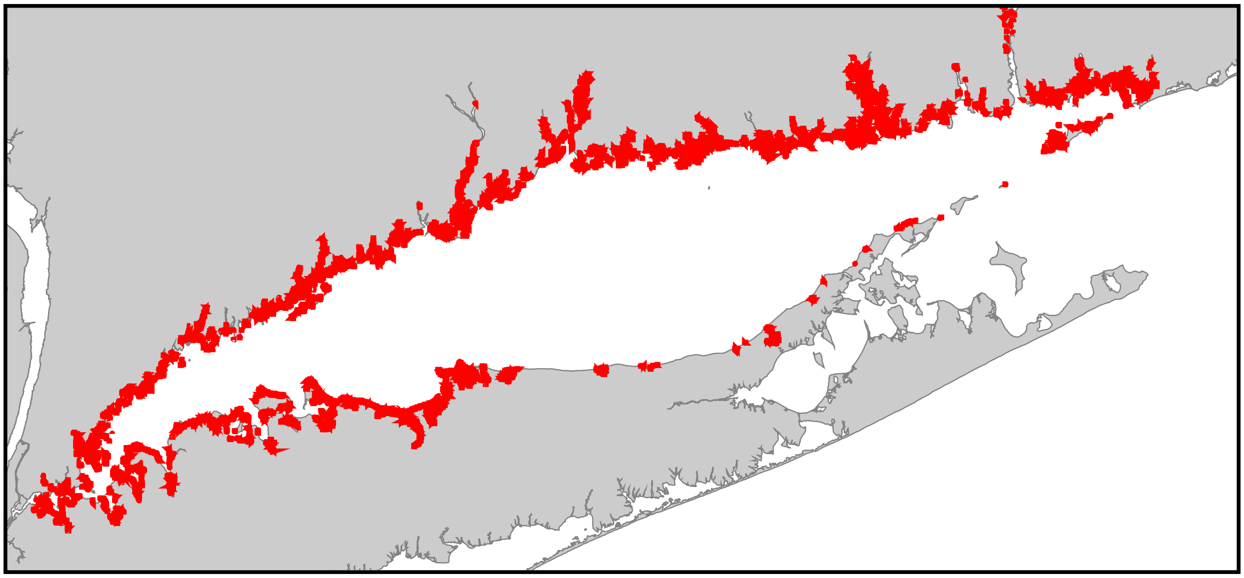


Figure 5. Distribution of sand and mud flats. Data were derived from Environmental Sensitivity Index GIS maps obtained from the NOAA Office of Response and Restoration (http://response.rerstoration.noaa.gov/esi).

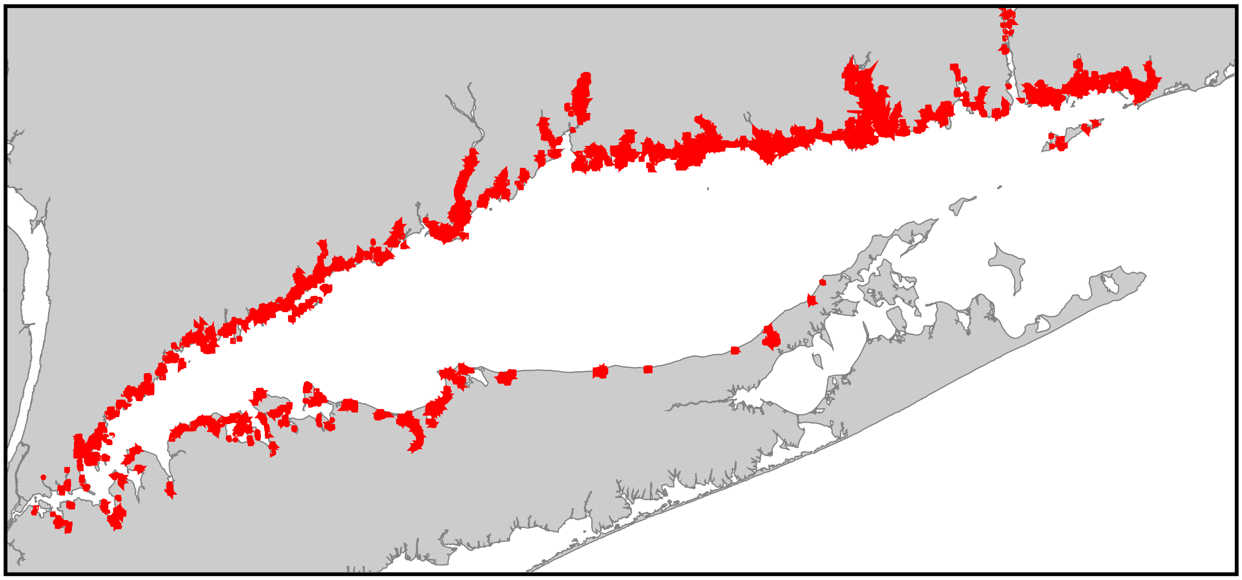


Figure 6. Distribution of salt marshes. Data were derived from Environmental Sensitivity Index GIS maps obtained from the NOAA Office of Response and Restoration (http://response.rerstoration.noaa.gov/esi).

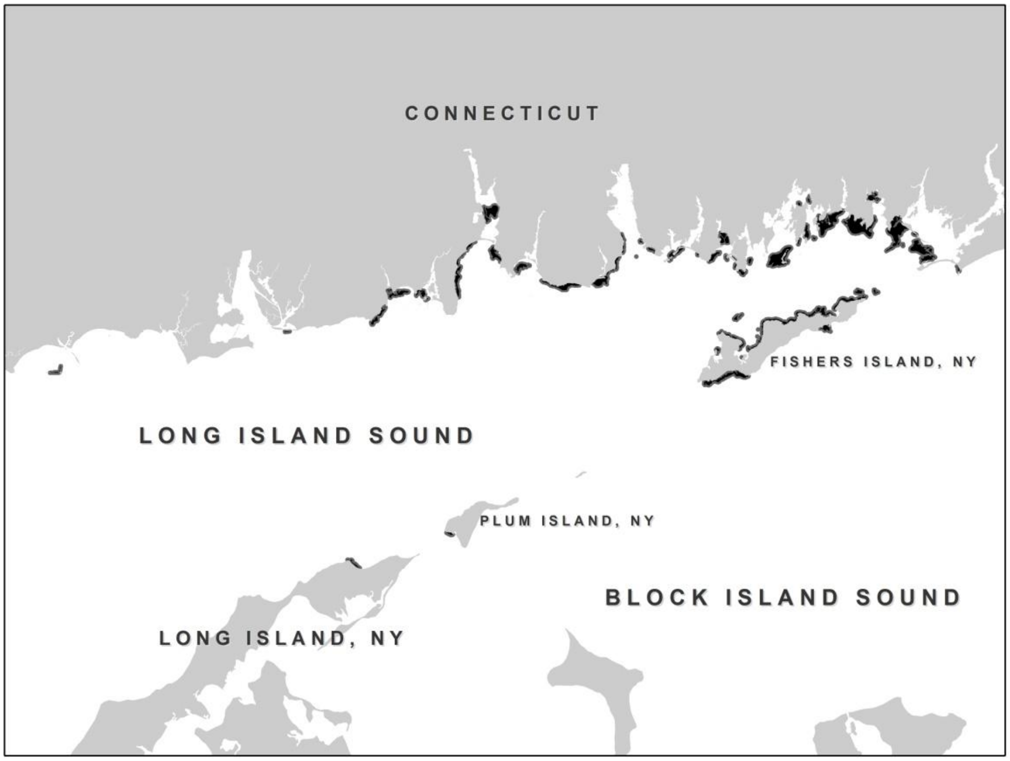


Figure 7. Map of the current eelgrass (*Zostera marina*) distribution in Long Island Sound adapted from Tiner et al. (2010). Meadow polygons were enlarged with a 400’ buffer to increase visibility in this format. Map provided by Lorne Brousseau, CCE.

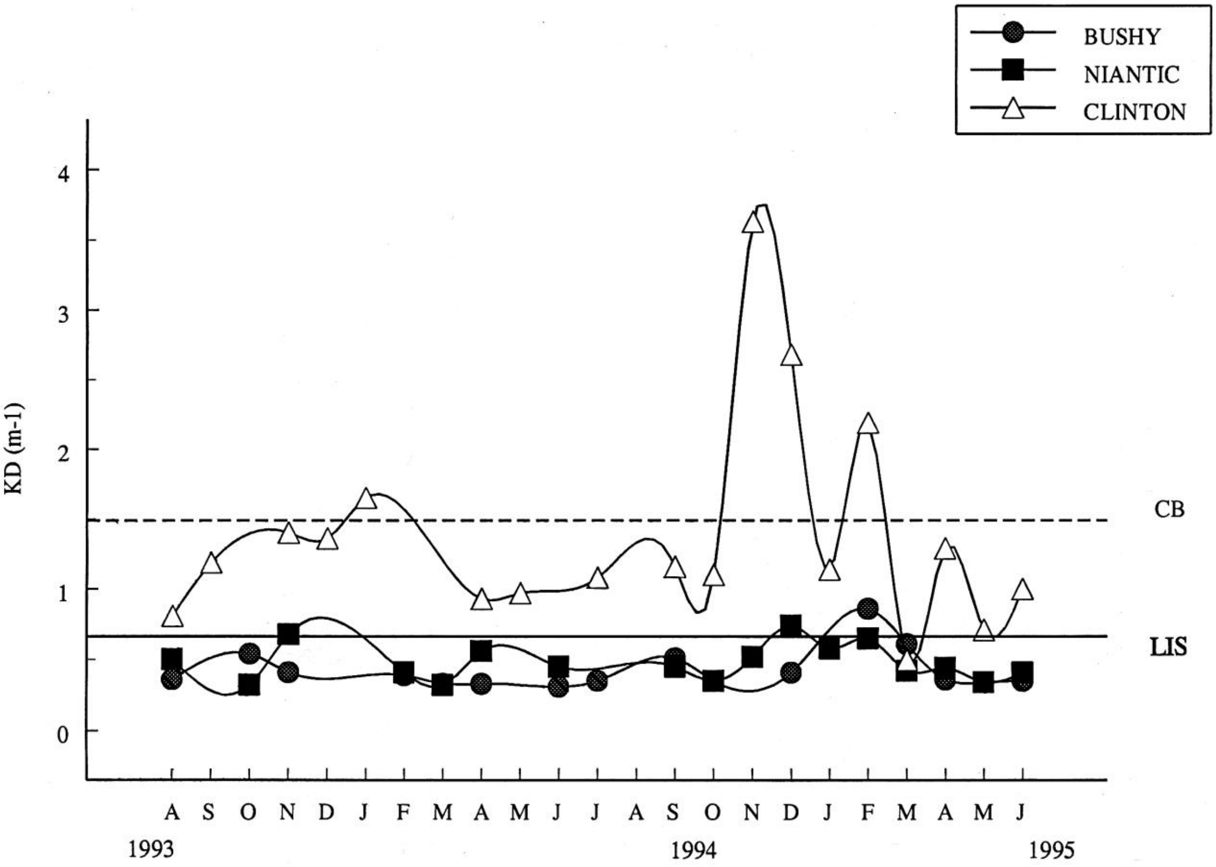


Figure 8. Temporal variation in K_d at three *Zostera marina* sites (Bushy Point, Niantic Bay and Clinton Harbor) along the Connecticut coast. The solid and dotted lines indicate values suggested as standard habitat requirements for eelgrass in Long Island Sound (LIS) and Chesapeake Bay (CB). From Yarish et al. (2006).

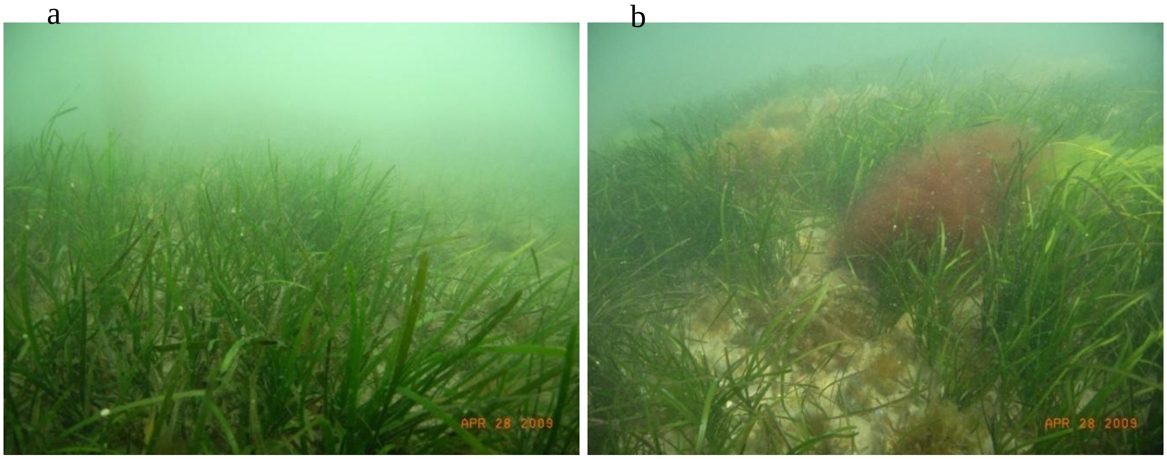


Figure 9. Restored meadows during early spring when the leaves are still short. (a) St. Thomas Point, East Marion, NY. This site was first planted in 2003 and involved using transplants from several donor meadows in the region. Depth at this site ranges from 2.5 m to 3.5 m at low tide. (b) Terry's Point, Orient, NY. This meadow was planted using plants from two natural donor meadows; Orient Point in the Peconic Estuary and Mulford Point in LIS. Depth at this site is 1.5 m at low tide (Photo credits: Chris Pickerell, CCE).

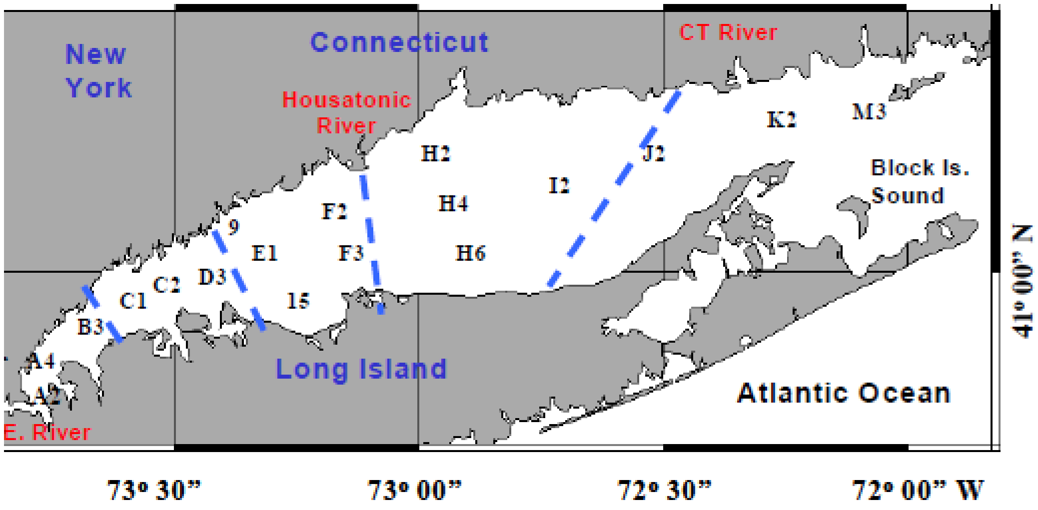


Figure 10. Sampling stations for the CT DEEP Water Quality Monitoring Program. Stations are the same as those sampled in 1988-1989 by the Long Island Sound Study. Blue dashed lines indicate boundaries between regions (after Kaputa and Olson 2000).

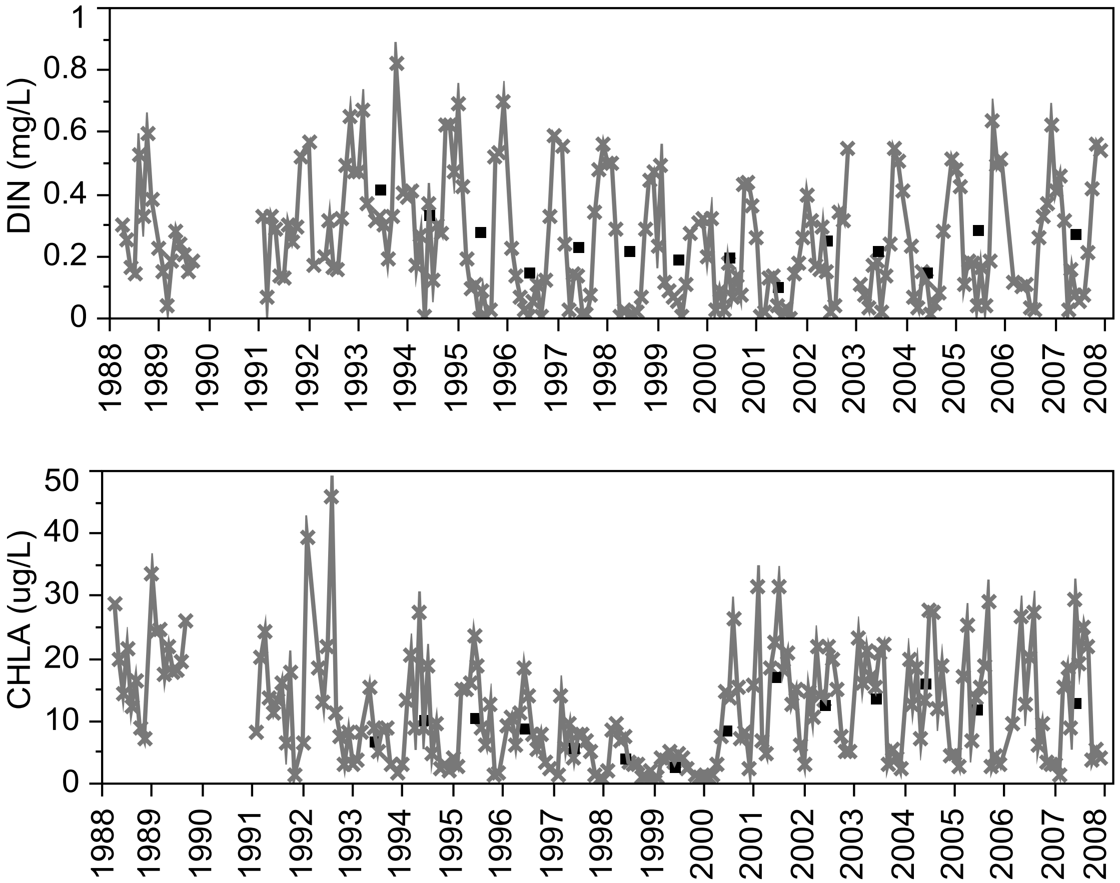


Figure 11. Monthly means (crosses) and annual means (squares) in dissolved inorganic nitrogen, DIN (top) and f chlorophyll (bottom) from 1988-2007 in the West Narrows surface waters. Data are from the Long Island Sound Study (1988-1989) and from the CT DEEP Water Quality Monitoring program (Dam et al. 2010). Annual means are shown only if 10 or more months were sampled in a particular year, and if the missing months were neither consecutive nor both January and December. Non-detectable data points were assumed to be 25% of the detection limit. There is a hint of a linear decrease of DIN: slope = -0.01 $mgL^{-1}y^{-1}$, r^2= 0.24, p = 0.084. The slope does not change even if the non-detectable points are assumed to be 0% of the detection limit.

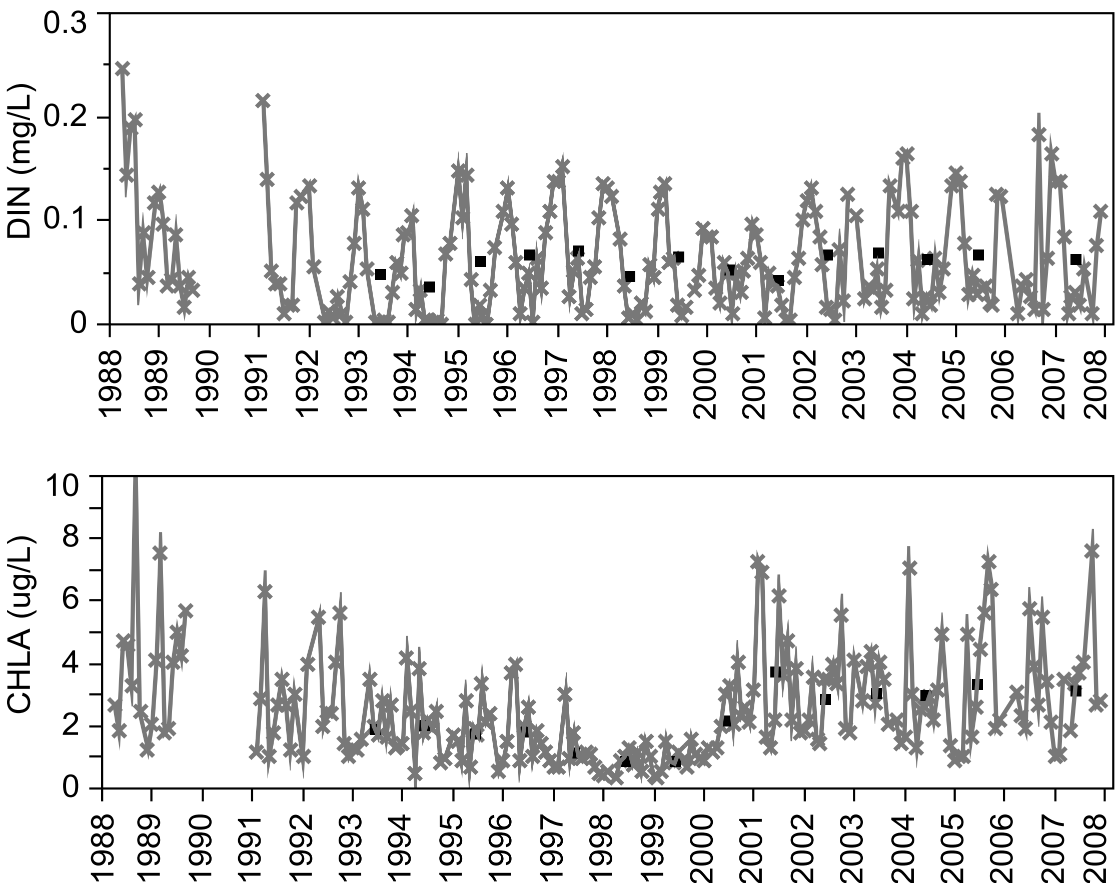


Figure 12. Monthly means (crosses) and annual means (squares) in chlorophyll (top) and dissolved inorganic nitrogen, DIN (bottom) from 1988-2007 in the East Basin surface waters. Details as in caption of Fig. 11.

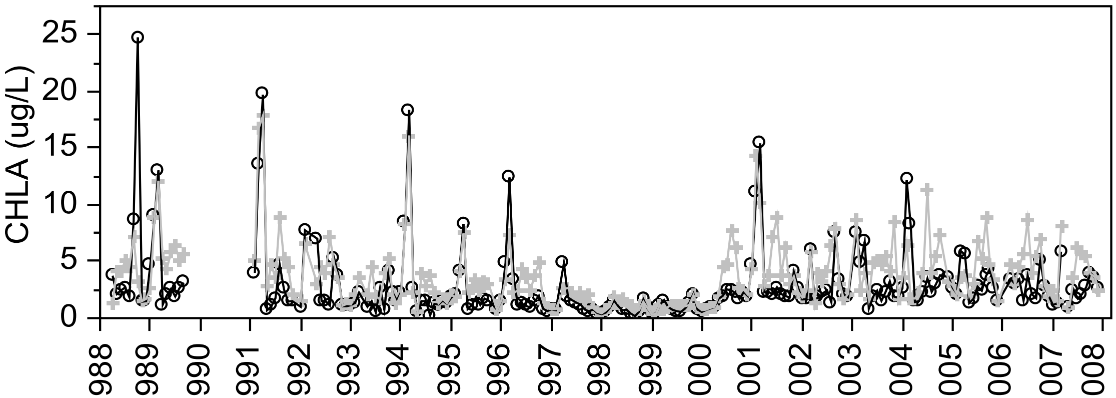


Figure 13. Chlorophyll concentration (µgL^{-1}) in the Central Basin of Long Island Sound. Circles represent surface waters and crosses represent bottom waters. Details as in caption of Fig. 11.

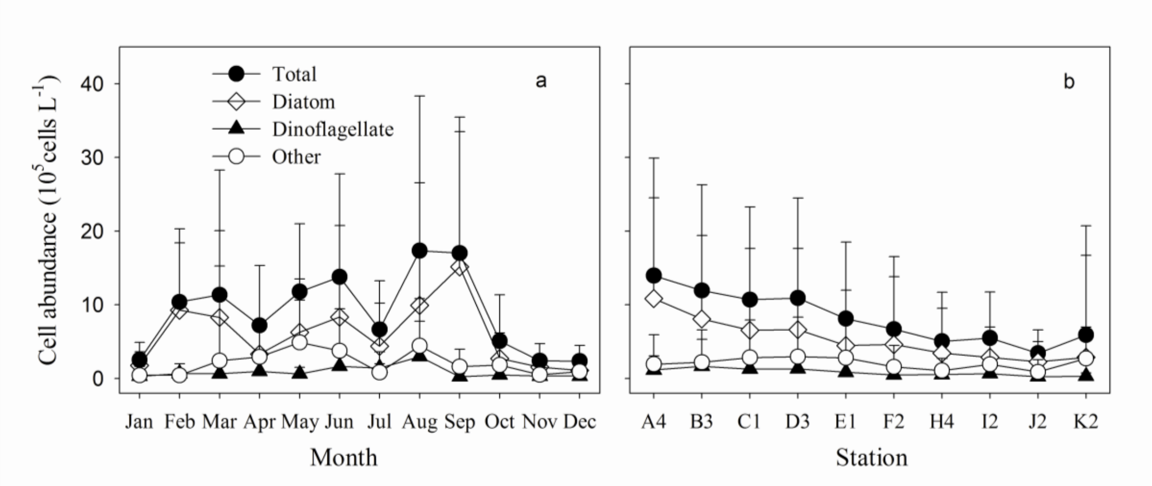


Figure 14. Temporal (panel a) and spatial variation (panel b) of phytoplankton community structure in LIS between 2002 and 2010. Shown are means and standard deviations (error bars). Data from the CT DEEP Water Quality Monitoring program (S. Lin, unpublished).

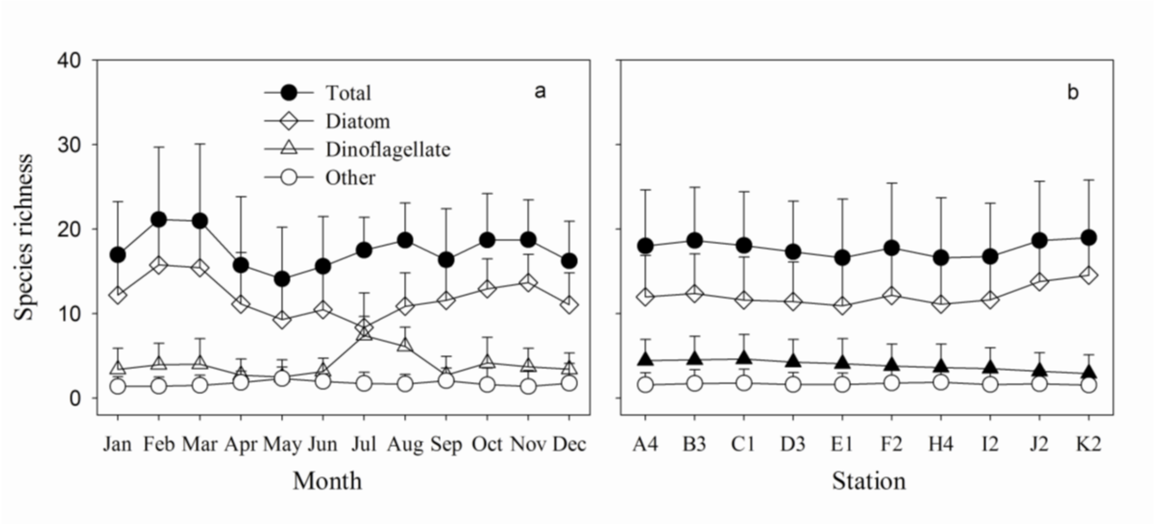
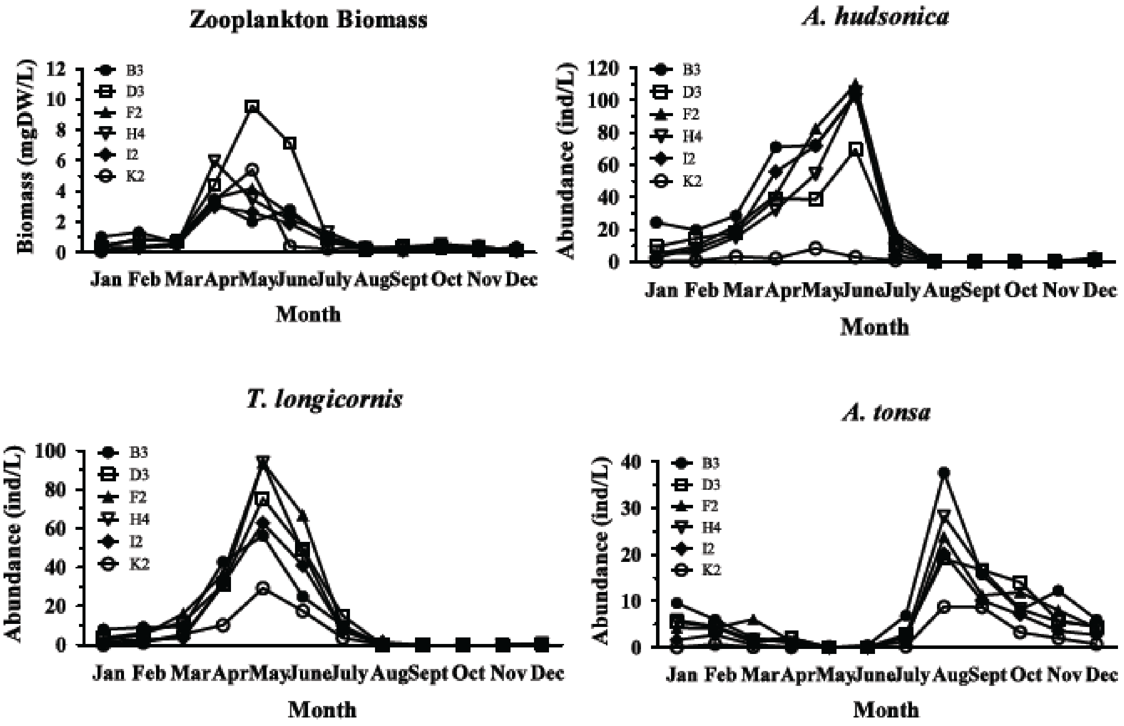


Figure 15. Temporal and spatial variation of cell abundance of phytoplankton in LIS between 2002 and 2010. Shown are means and standard deviations (error bars). Data from the CT DEEP Water Quality Monitoring program (S. Lin, unpublished).



Zooplankton Biomass

A. hudsonica

T. longicornis

A. tonsa

Figure 16. Mesozoplankton in Long Island Sound. Shown are climatology plots for the period 2002-2009. The upper left plot is for total biomass (determined directly from aliquots of samples). The other plots are for abundance of the dominant zooplankton species. For station locations, see Fig. 10. Data from the CT DEEP zooplankton Monitoring program (Dam and McManus 2009).

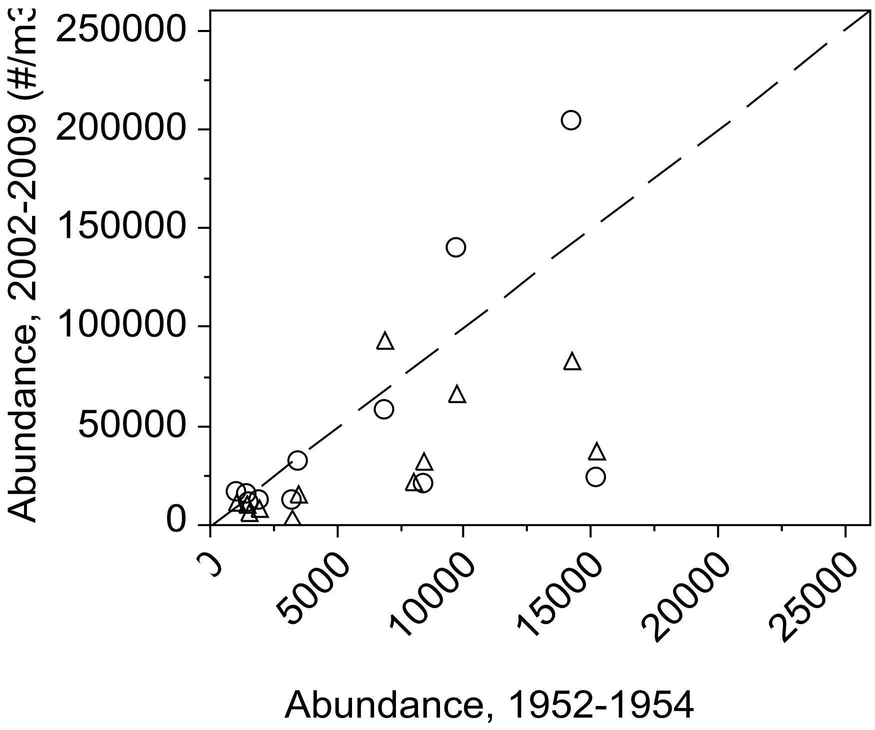
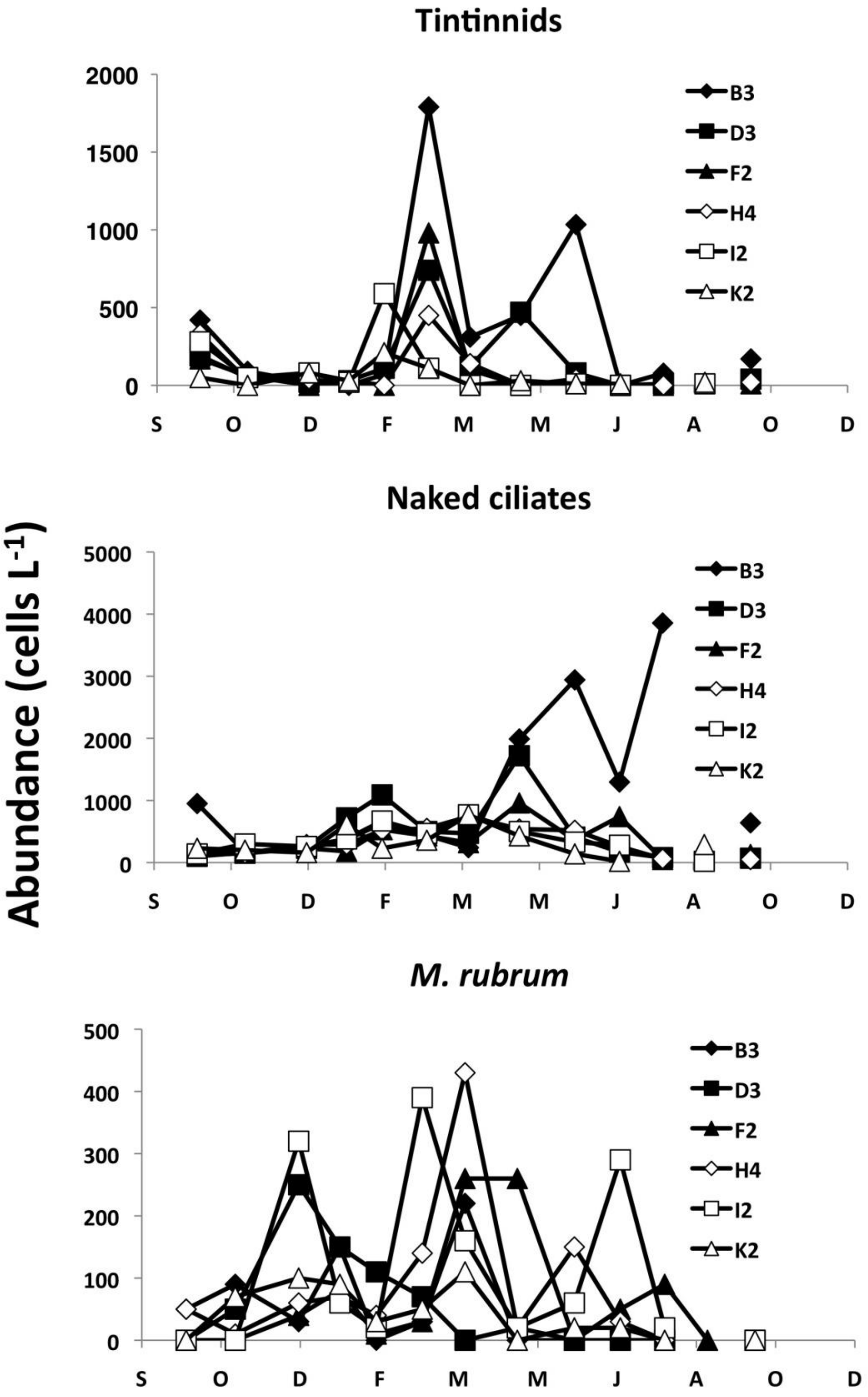


Figure 17. Mean monthly zooplankton abundance (No. m^{-3}) at station H4 for 1952-53 (Deevey 1956) versus 2002-2004 and 2008-2009 (Dam and McManus 2009). Dashed line indicates 1:1 relationship. Triangles = years 2002-2004, circles = years 2008-2009.



Tintinnids

Naked ciliates

M. rubrum

Figure 18. Abundances of tintinnids (top), other heterotrophic ciliates (middle), and the autotrophic ciliate *Mesodinium rubrum* (=*Myrionecta rubra*) for 2008-2009. For station locations see Fig. 10. Data from the CT DEEP zooplankton Monitoring program.

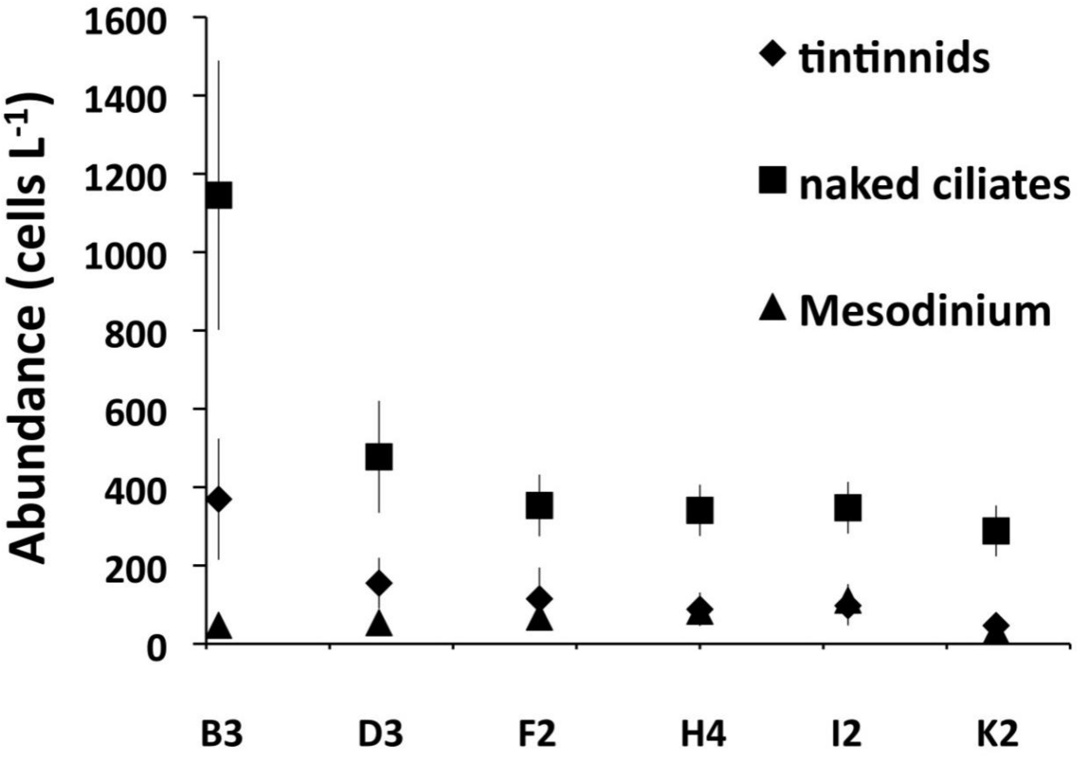


Figure 19. Abundances of ciliates (individuals per L), plotted as annual averages by station for the period 2008-2009. (from Dam and McManus 2009).

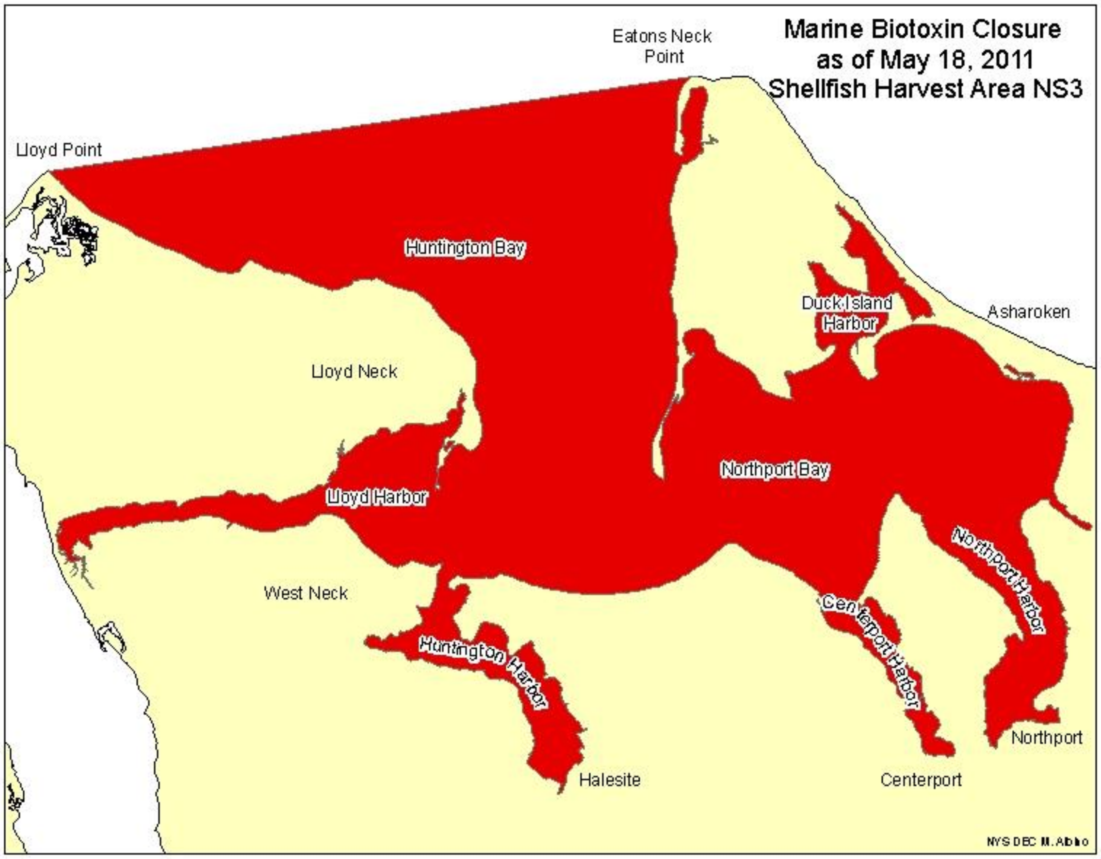


Figure 20. Shellfish beds (~10,000 acres) in Huntington and Northport Bays closed by the NYSDEC due to PSP production by *A. fundyense* in 2011. This region was never closed due to PSP prior to 2006, but has been closed in 2006, 2008, 2009, 2010, and 2011 due to saxitoxin contamination of shellfish during *A. fundyense* blooms.

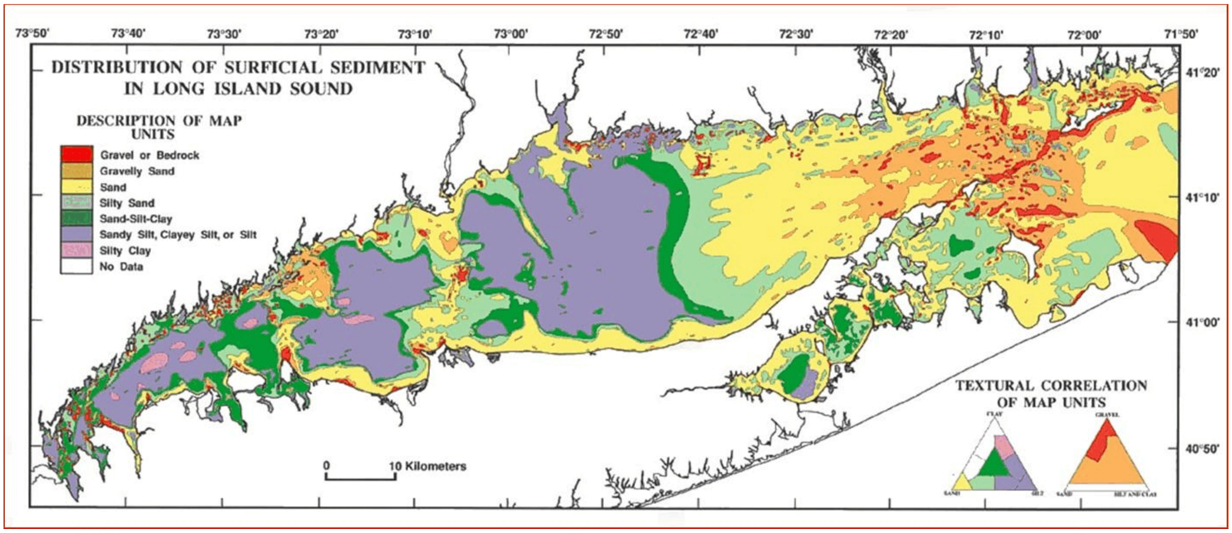


Figure 21. Distribution of seafloor habitat / patch types in LIS based on sediment texture. Map is from Poppe et al. (2000).

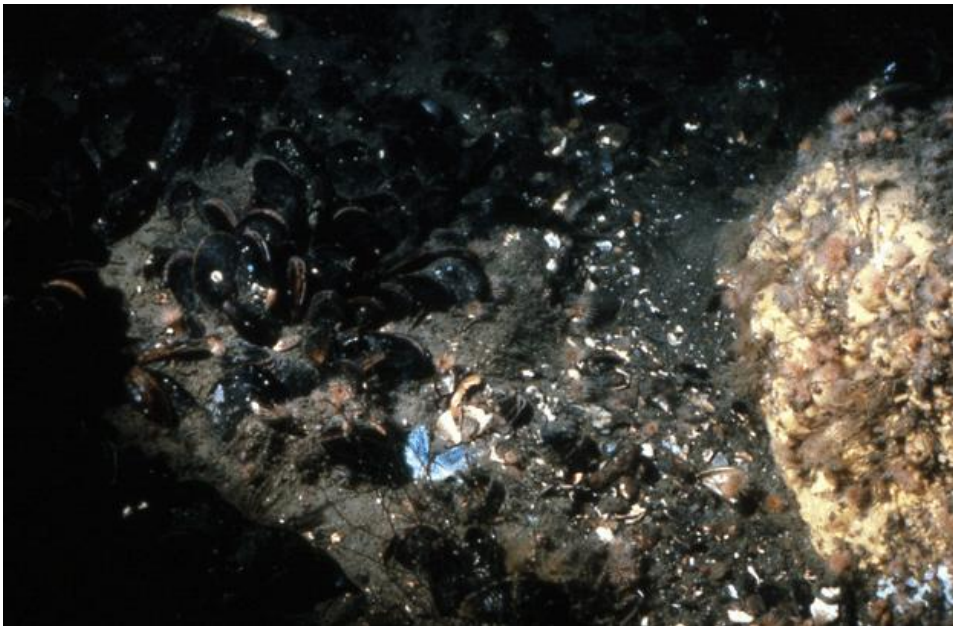


Figure 22. Image of small scale biogenic and physical features that increase habitat complexity on portions of LIS. Note mussels forming clumps on sediment and a portion of a boulder to the right with various fouling organisms. At the base of the boulder is an accumulation of shell hash. Largest mussels are ~ 2 - 3 cm in length for scale.

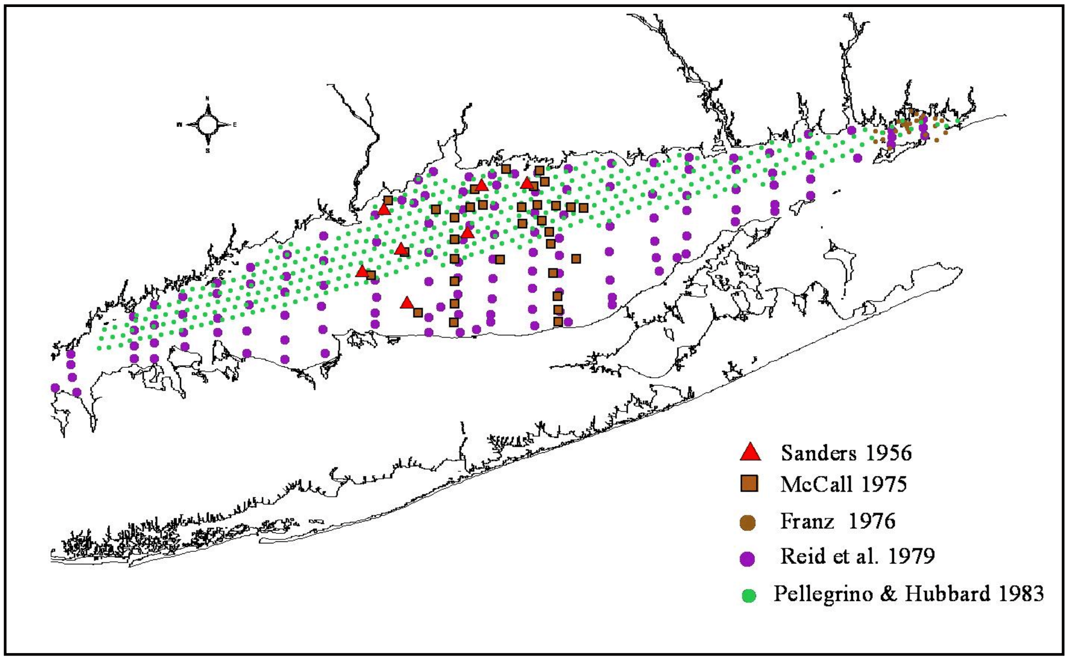


Figure 23. Benthic community surveys in the deeper water portions of LIS conducted prior to 1985. See text for details.

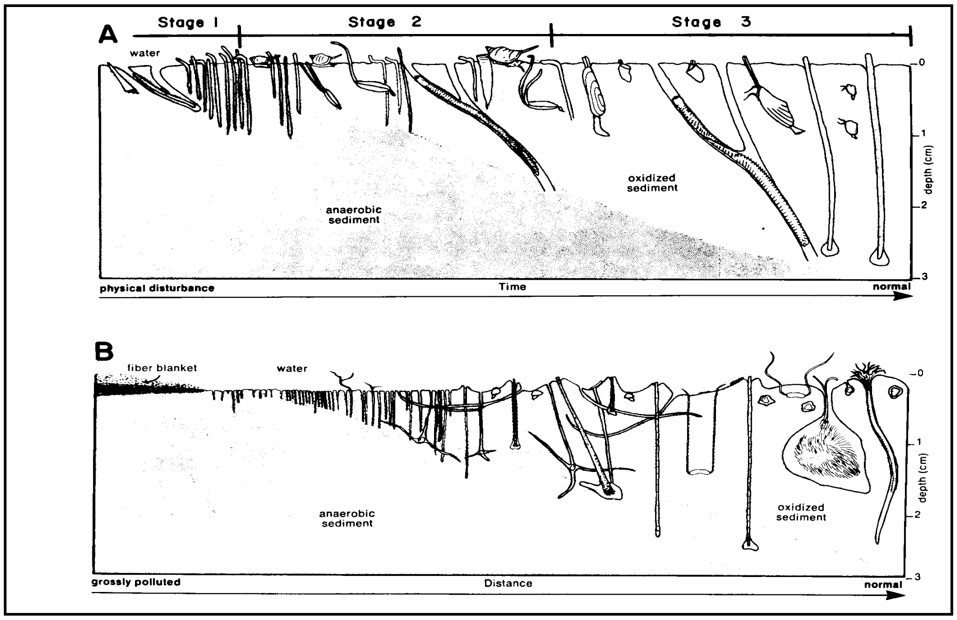


Figure 24. A) Model of soft-sediment succession proposed by Rhoads et al. (1978) in which disturbance is followed by recolonization of stage I species comprised of opportunistic species which live in the upper few cms of the sediment. Eventually a “climax” Stage 3 community is reestablished comprised of deeper dwelling more K-selected type species. The successional model stages have similarities to responses of infauna along an organic pollution gradient as proposed by Pearson and Rosenberg (1978) shown in B.

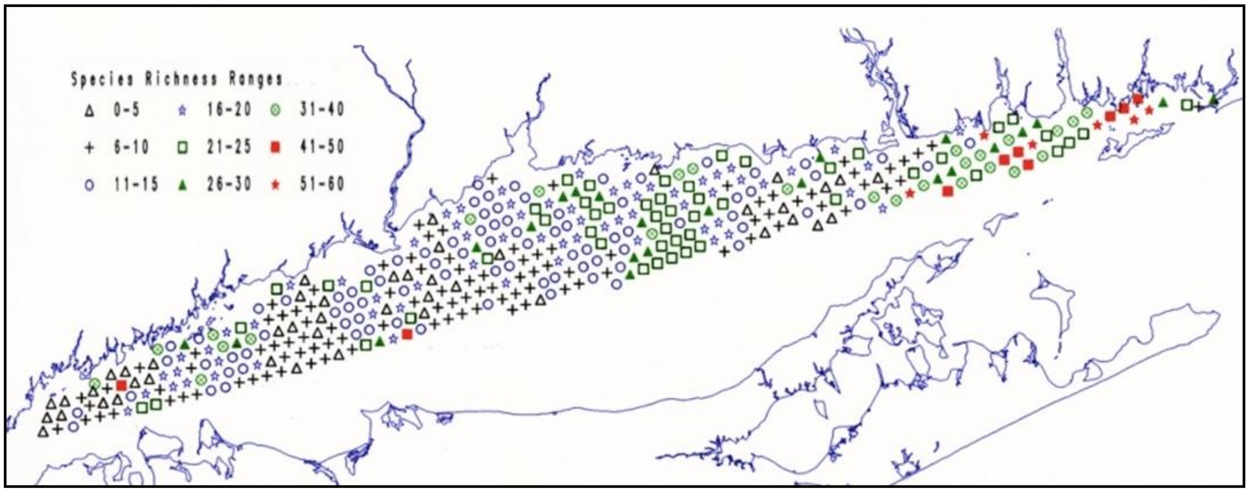


Figure 25. Spatial patterns of species richness in LIS based on data presented in Pellegrino and Hubbard (1983). Values represent the total number of species per 0.04 m^2 grab sample.

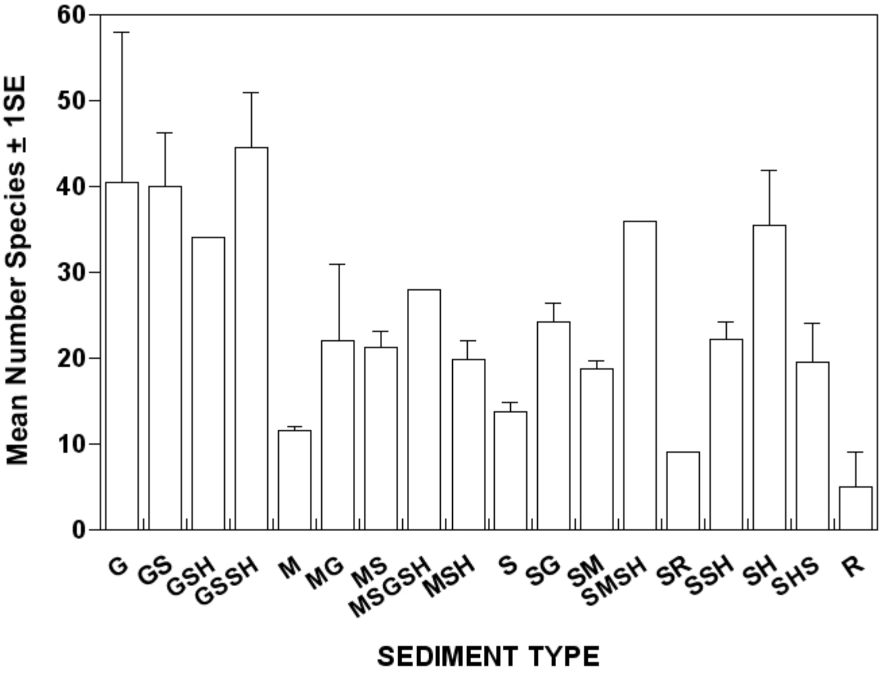


Figure 26. Relationship between species richness and sediment type in LIS. The values represent the mean number of species per sample at stations with the same bulk sediment characteristics identified by Pellegrino and Hubbard (1983) Sediment type designations are as follows: G - Gravel; GS - Gravel, Sand; GSH - Gravel, Shell; GSSH - Gravel, Sand, Shell; M - Mud; MG - Mud, Gravel; MS - Muddy Sand; MSGSH - Muddy sand, Gravel, Shell; MSH - Mud, Shell; S - Sand; SG - Sand, Gravel; SM-Sandy mud; SMSH - Sandy mud, Shell; SR - Sand, Rocks; SSH - Sand, Shell; SH - Shell; SHS - Shell, Sand; R - Rocky

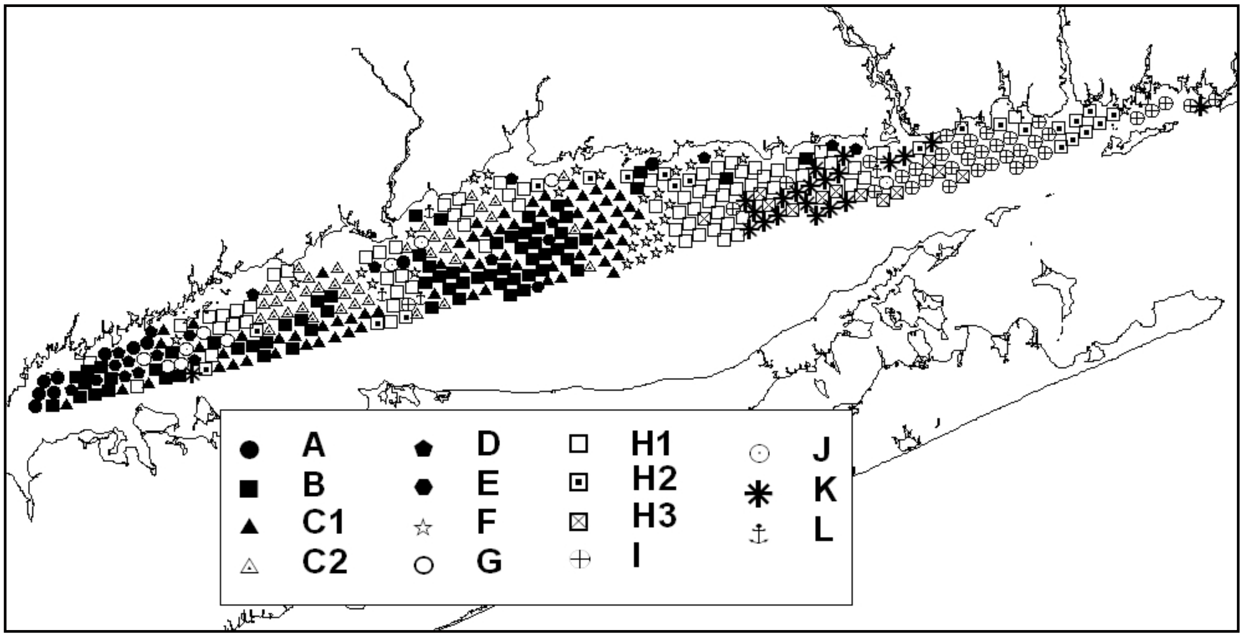
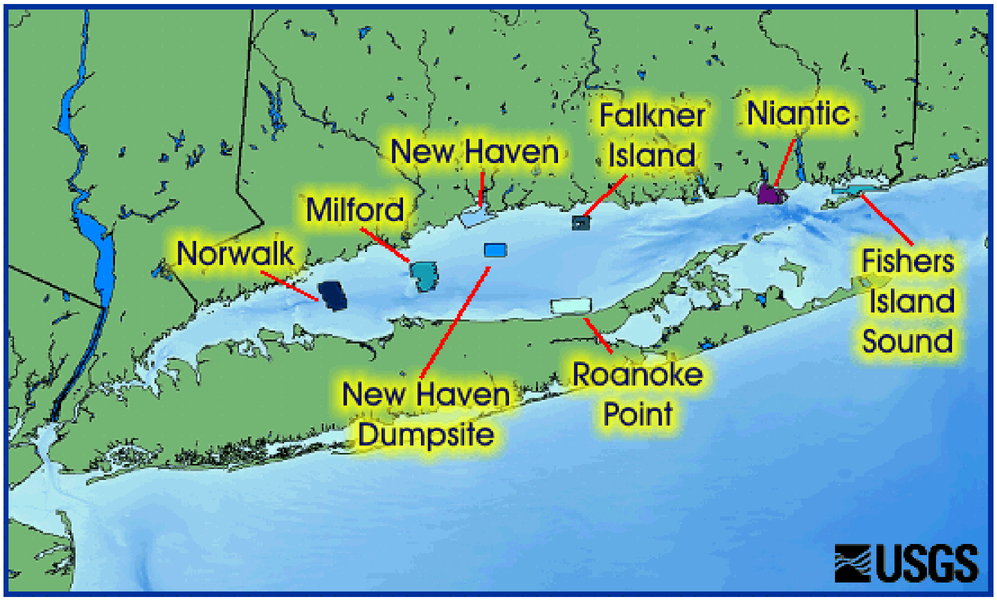


Figure 27. Spatial distribution of benthic communities identified via clustering analysis by Zajac et al (2000) of data provided in Pellegrino and Hubbard (1983).



Map showing location of Long Island Sound sidescan sonar mosaics. Select the mosaic area name from the table below to view the associated metadata file.

Figure 28. Locations of USGS side scan mosaic study areas in LIS. See also USGS website for up to date overview of USGS and NOAA sea floor mapping in LIS.

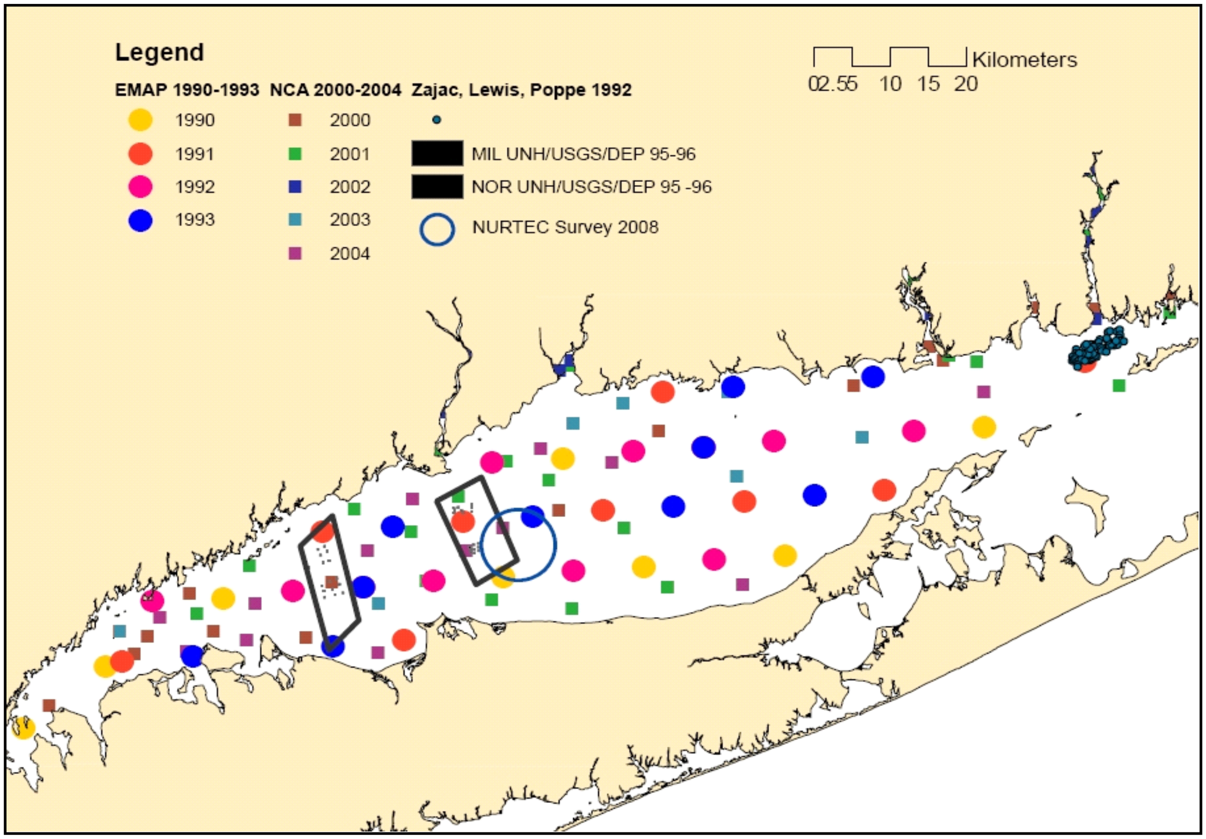


Figure 29. Location of benthic surveys and studies in LIS conducted between 1985 and 2010 (some studies may not be shown); does not include inshore / intertidal studies.

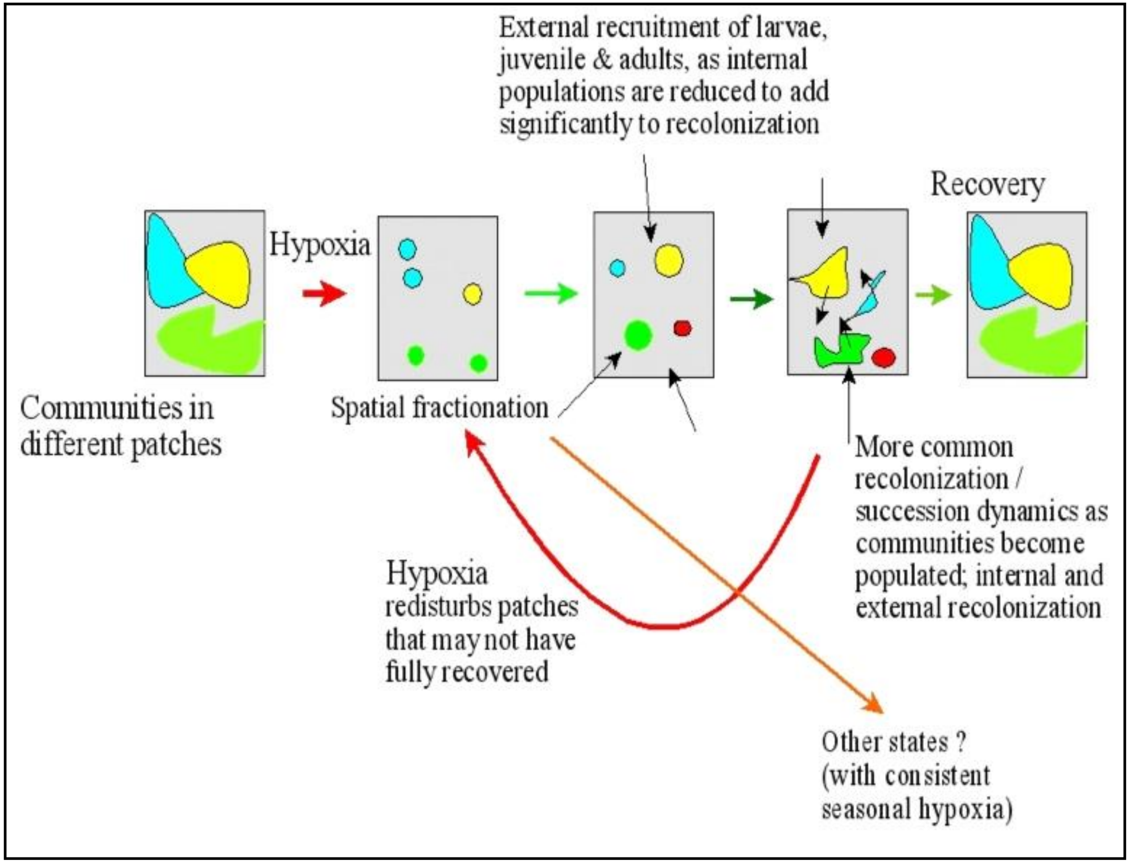


Figure 30. Model of potential responses to large-scale disturbances in soft-sediment benthic landscapes. Because of increased spatial variation in remnant community structure, initial recolonization patterns may also be variable and not follow the patterns predicted by models developed from small-scale experimental work. There may be some temporal lag as to when more typical successional patterns are evident as biotic patches reach critical abundance levels so as to make significant contributions to recolonization of the overall disturbed portion of the benthic landscape. If hypoxia is recurrent, there may be an overall, long-term shift in community structure. Modified from Zajac (1998).

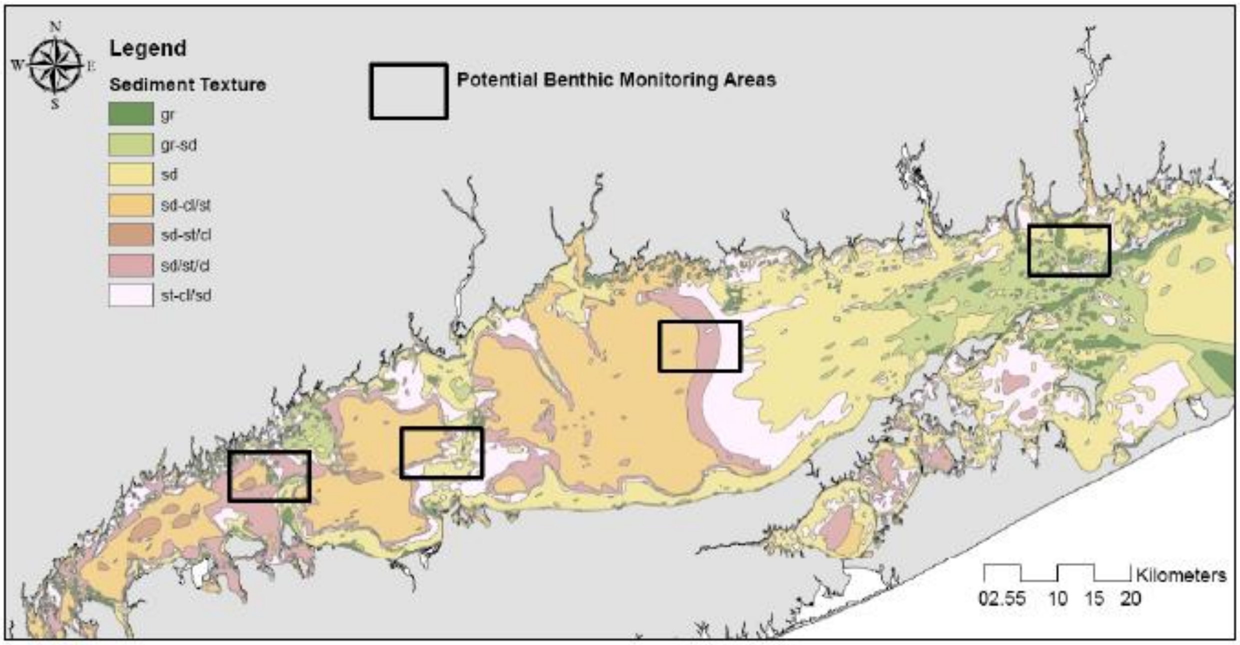


Figure 31. Potential, long-term benthic monitoring areas in Long Island Sound. Each area is comprised of several types of sedimentary habitats and together employ a natural gradient "experimental" design. Their location at the transitions among different regions of the Sound would integrate with the known distributions of benthic community types.

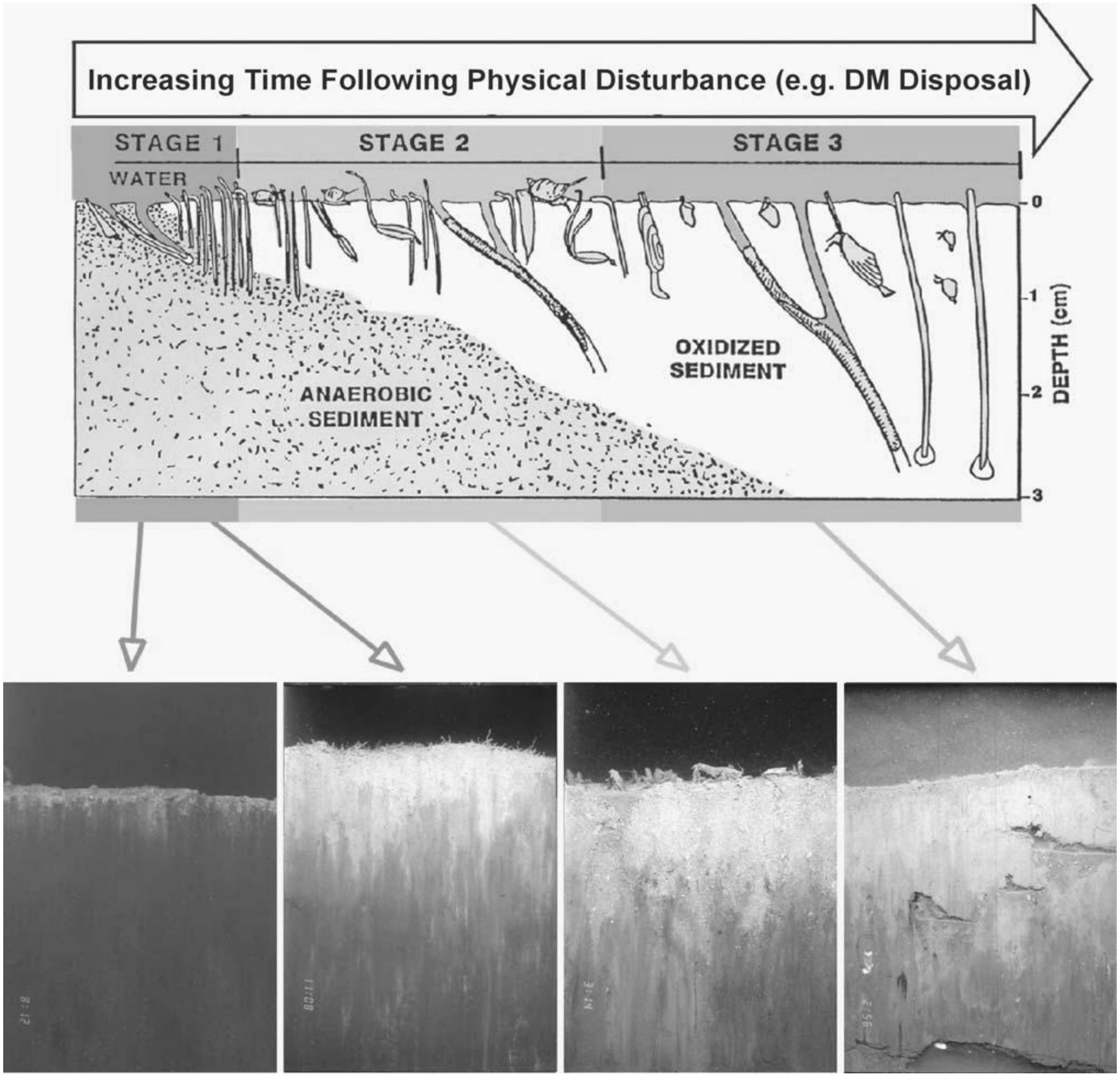


Figure 32. The drawing at the top (from Figure 24) illustrates the development of infaunal successional stages over time following a physical disturbance. The SPI images below the drawing provide examples of the different successional stages. (A) Highly-reduced sediment with a very shallow RPD layer (contrast between light colored surface sediments and dark underlying sediments) and little evidence of infauna. (B) Numerous small polychaete tubes are visible at the sediment surface (Stage 1) with a slightly deeper aRPD compared to the previous image. (C) A mixture of polychaete and amphipod tubes occurs at the sediment surface (Stage 2). (D). Numerous burrow openings and feeding pockets (voids) at depth within the sediment are evidence of deposit-feeding, Stage 3 infauna.(From Germano et al. 2011).

Figure 33. Hillshaded multibeam bathymetry of a portion of the Central Long Island Sound Disposal Site surveyed in 2009. Individual mounds (e.g., CLIS-05) represent accumulated disposal of dredged material for one or more disposal seasons (October-May). Relief is exaggerated to highlight low relief features that result from impact of dredged material on the seafloor (from Valente et al., 2010).

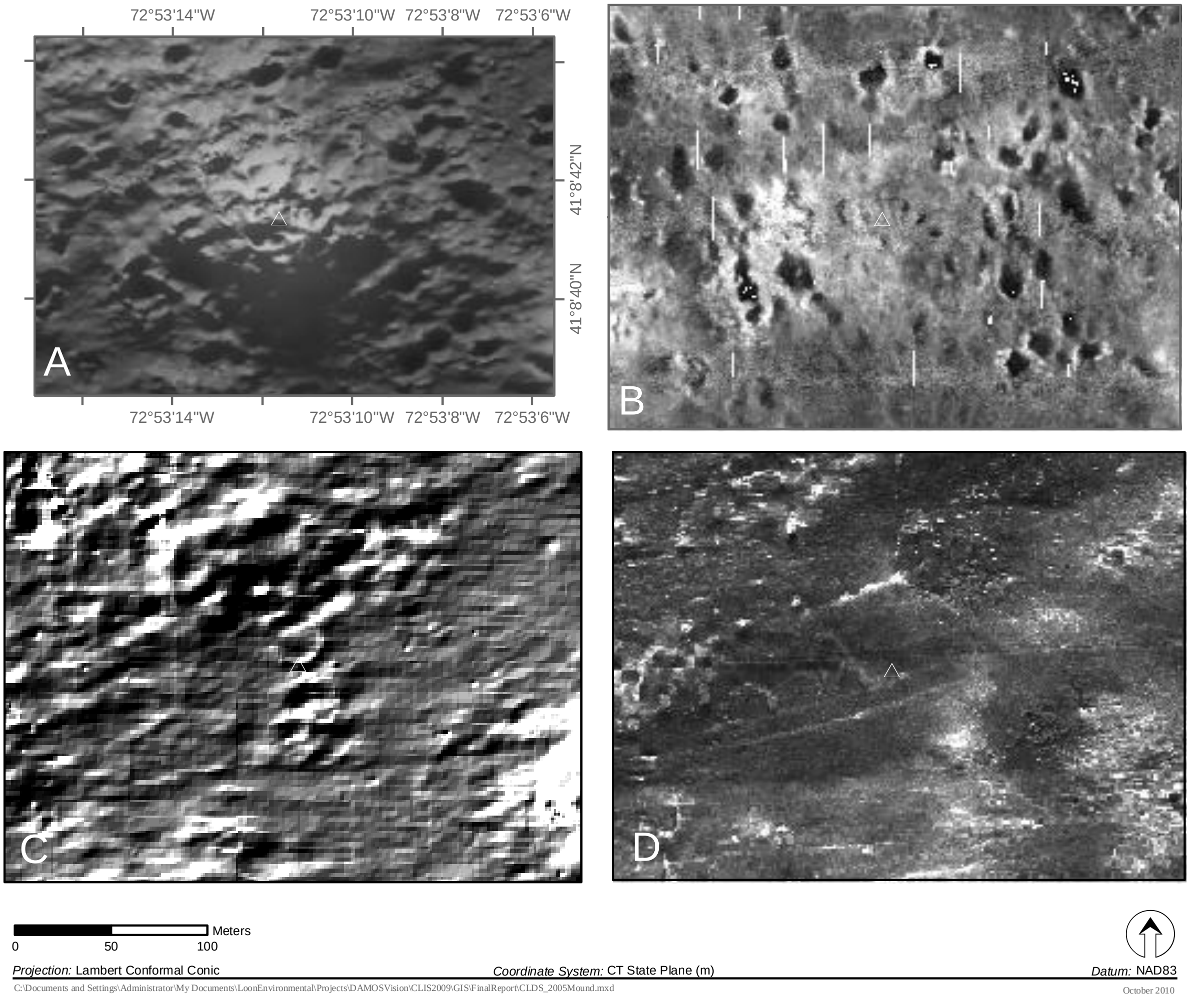


Figure 34. Surface features within a dredged material disposal site in Long Island Sound before and after several disposal seasons. Images are centered over the location of a mound (CLIS-05) formed from October 2005 to May 2006. A. Hillshaded multi-beam bathymetry from 2009, 3.5 years after mound formation. B. Backscatter mosaic (sidescan imagery) from multibeam survey from 2009. C. Hillshaded multi-beam bathymetry from 2005 prior to mound formation. D. Sidescan sonar mosaic from 1997 (from Poppe et al., 2001). Individual ring features and impact craters are from single disposal events with split-hull disposal barges (from Valente et al., 2010 and ENSR 2007).

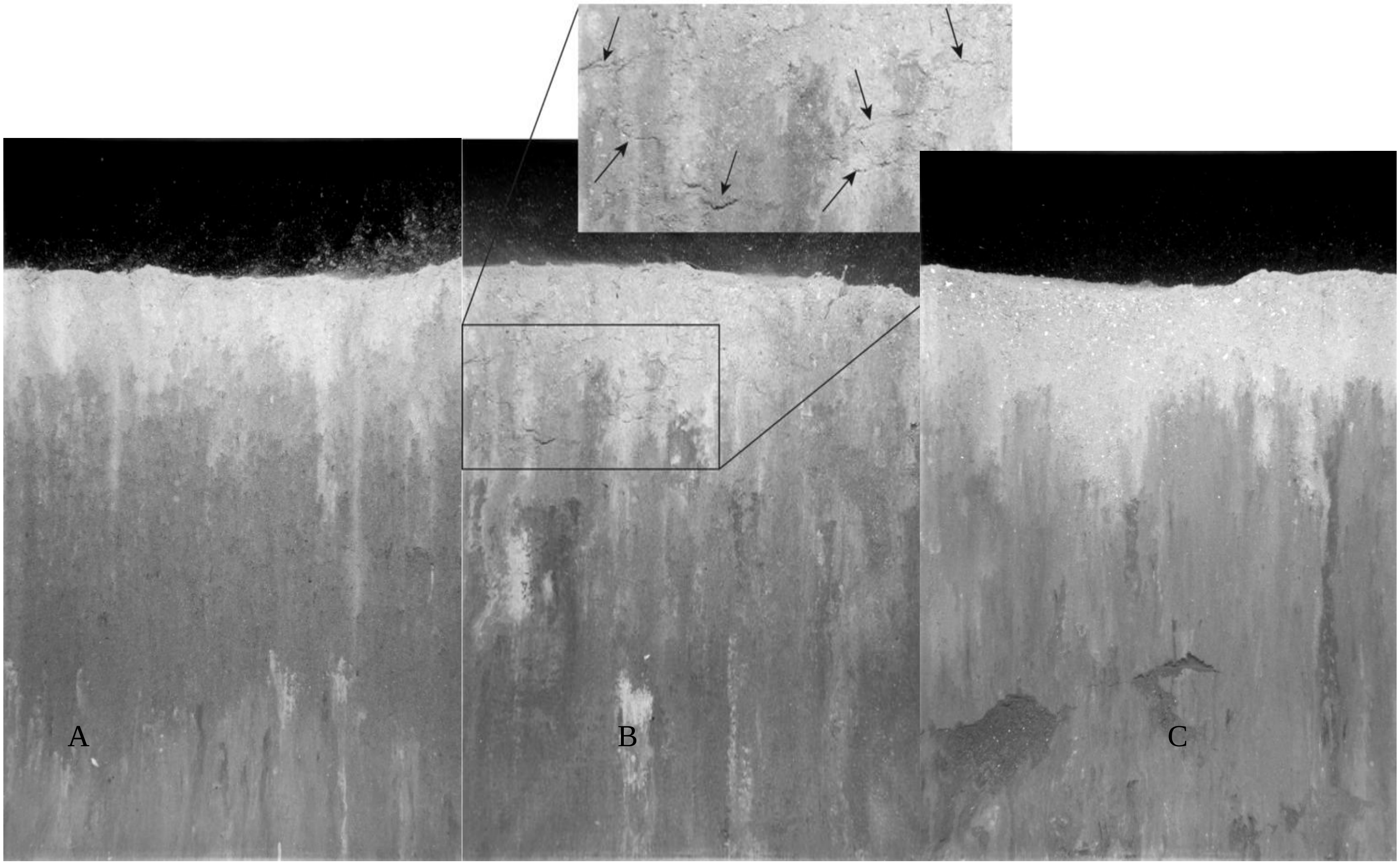


Figure 35. Sediment profile images collected in October 2009 from a disposal mound (CLIS-08) formed in from October 2008 to May 2009 at the Central Long Island Sound Disposal Site. A. Image illustrating dredged material colonized by tube-building worms (Stage 1). B. Image illustrating a transitional successional status from Stage 1 to 2. Small Stage 1 worm tubes are visible at the sediment surface, and numerous small tunnels produced by burrowing Stage 2 meiofauna (e.g., crustaceans and bivalves) occur just below the surface (arrows inset). C. Image showing a large vertical burrow and feeding voids (arrows) resulting in a Stage 3 successional designation (from Valente et al., 2010).

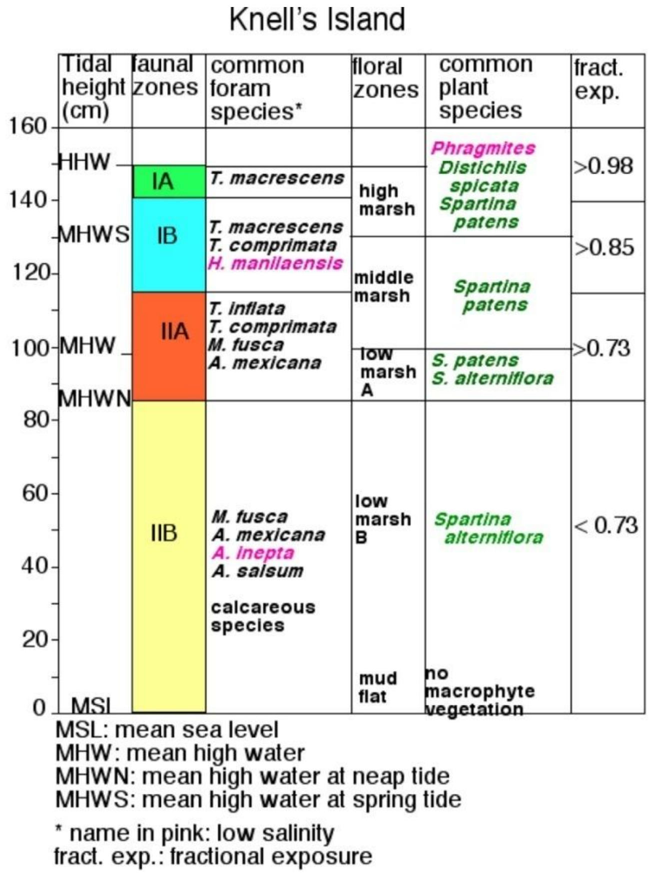


Figure 36. Foraminiferal zonation and plant zonation within the intertidal zone of the salt marshes at Knell's Island, Housatonic River.

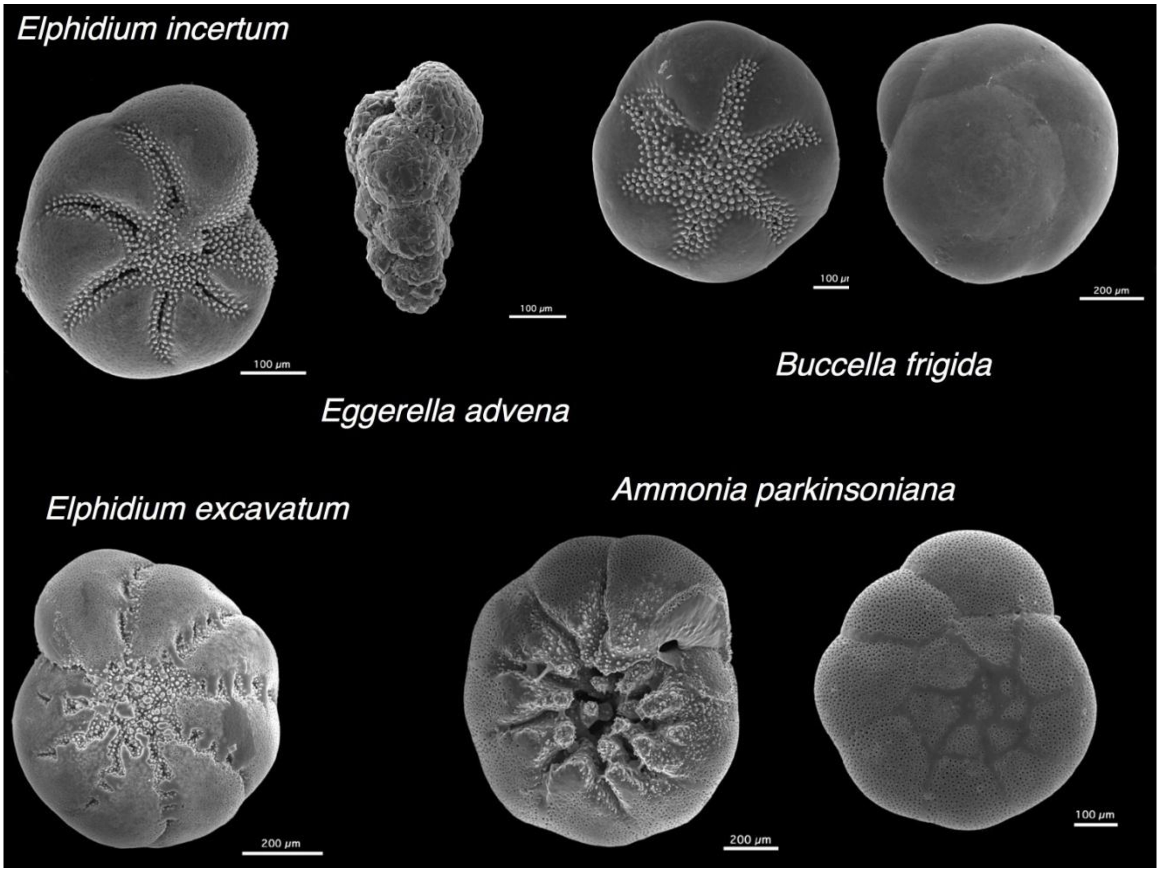


Figure 37. Most common benthic foraminiferal species in Long Island Sound. Both ventral and dorsal views are given for the two trcohospiral species, *Bucella frigida* and *Ammonia parkinsoniana*.

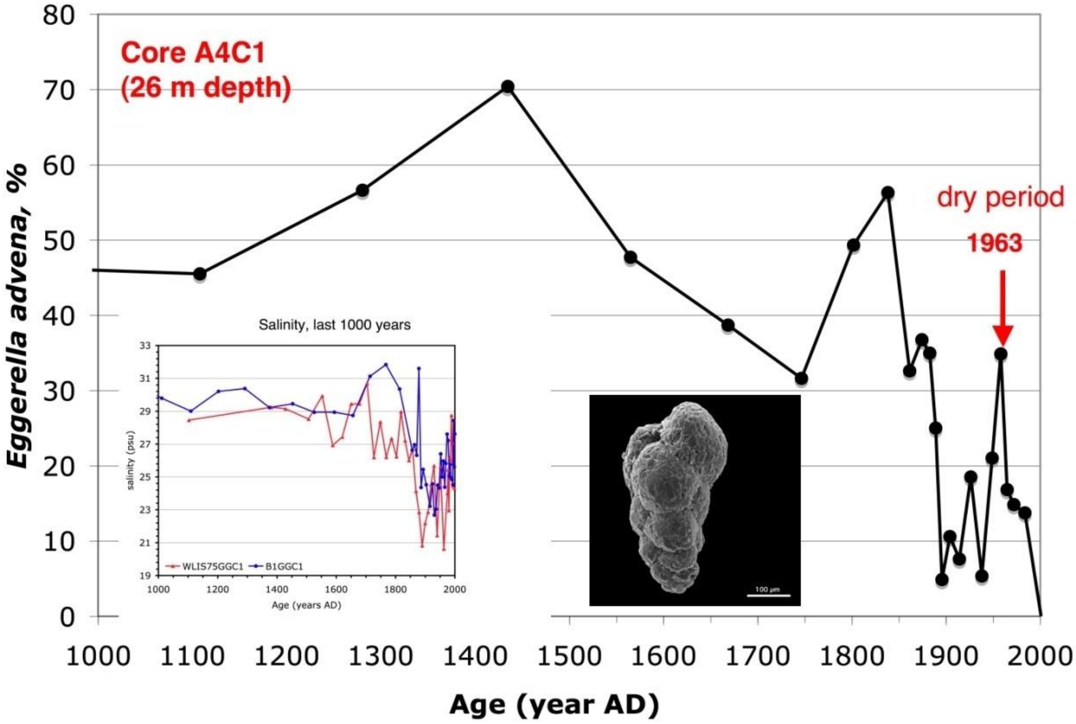


Figure 38. Relative abundance of *Eggerella advena* (shown in Scanning Electron Micrograph) for the last 1000 years, as observed in Core A4C1 (western LIS). Inset shows reconsgtructed salinity for the last 1000 years for cores WLIS 75GGC1 (The Narrows) and B1GGC2 (Outside the mouth of the Housatonic River).

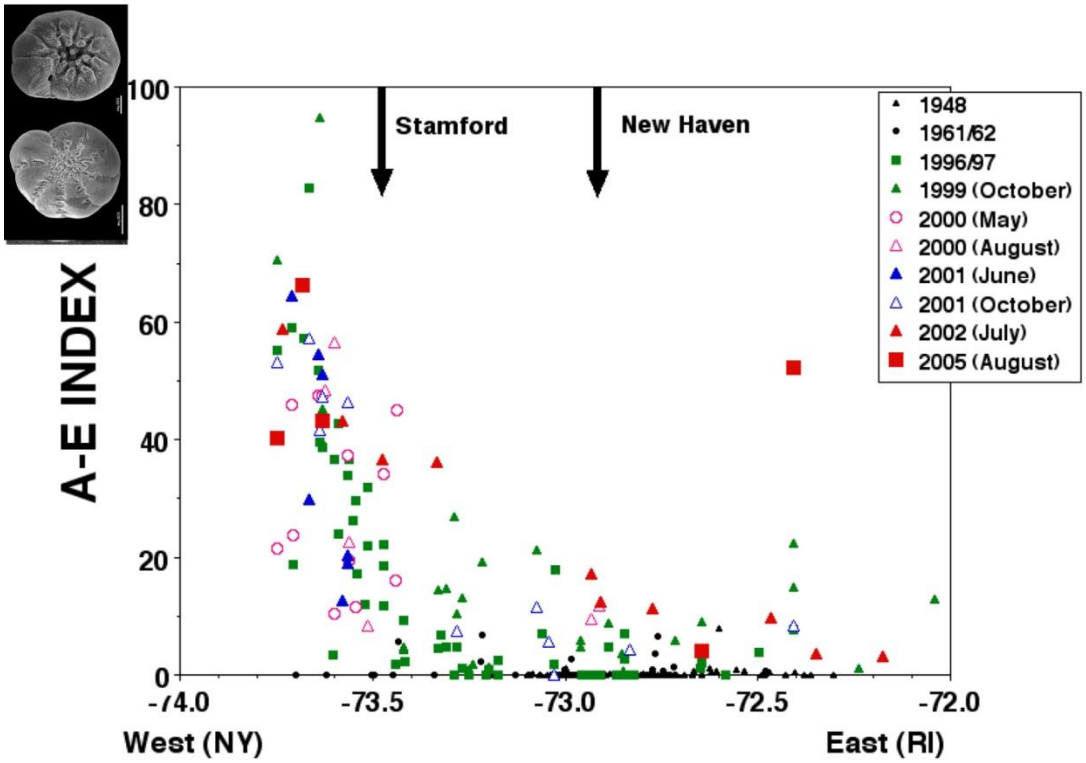


Figure 39. A-E index (percentage *Ammonia parkinsoniana* normalized to the sum of the percentages of *Ammonia* and *Elphidium* species) for foraminiferal assemblages in grab samples collected in various years; all samples plotted versus longitude (E-W). Upper Scanning Electron Micrograph: *Ammonia parkinsoniana*, ventral side; Lower Scanning Electron Micrograph: *Elphidium excavatum*

Figure 40. Connecticut Department of Energy and Environmental Protection commercial fishery landings data, 1995-2007.

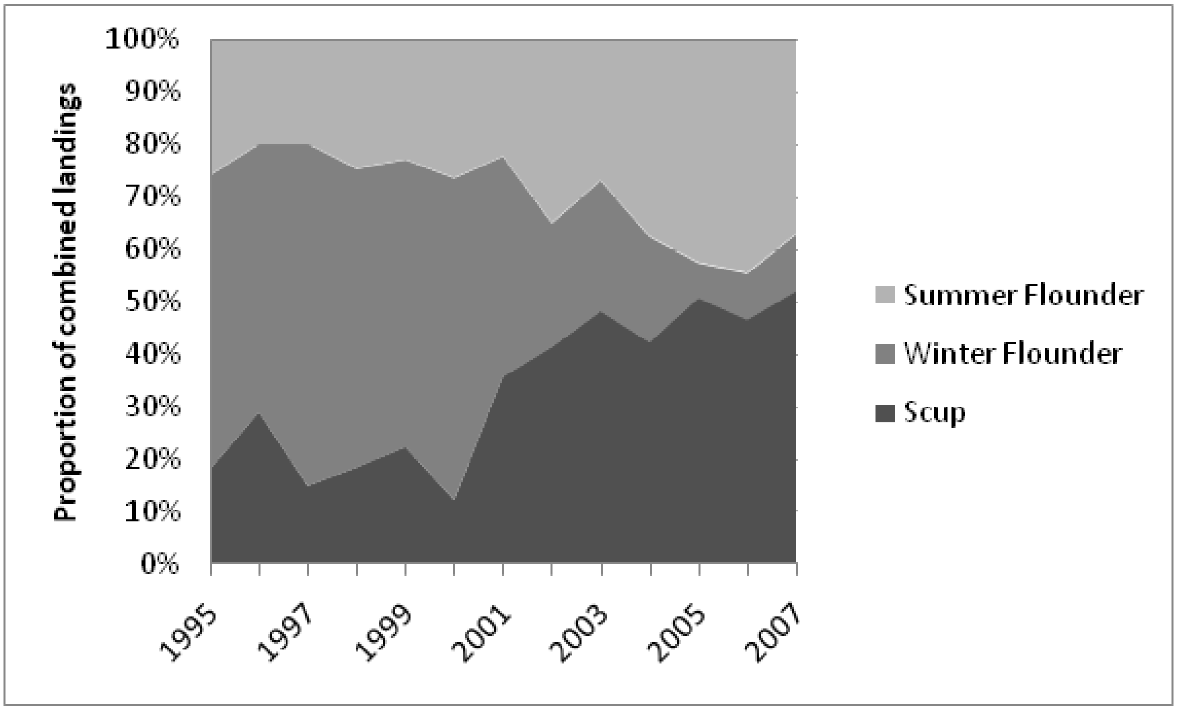


Figure 41. Proportion of commercial landings for summer flounder, winter flounder and scup, 1995-2007.

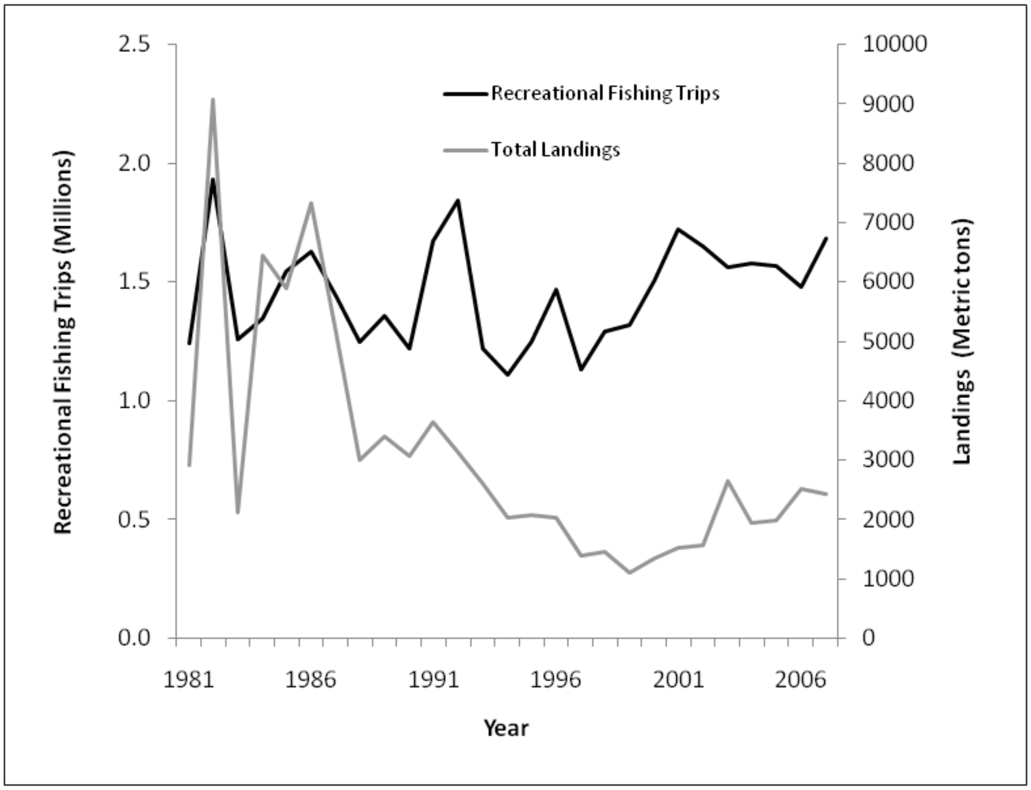


Figure 42. Recreational fishing effort and landings in LIS 1981-2007.

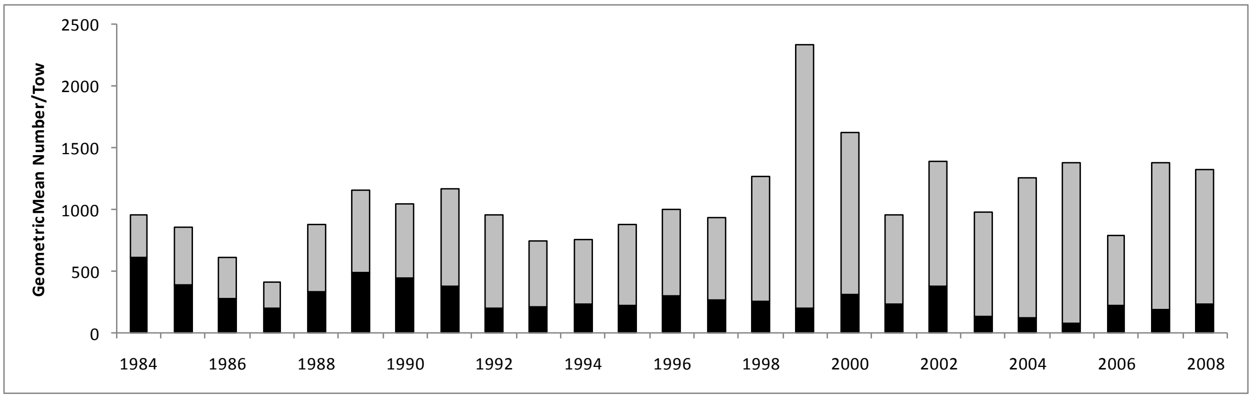
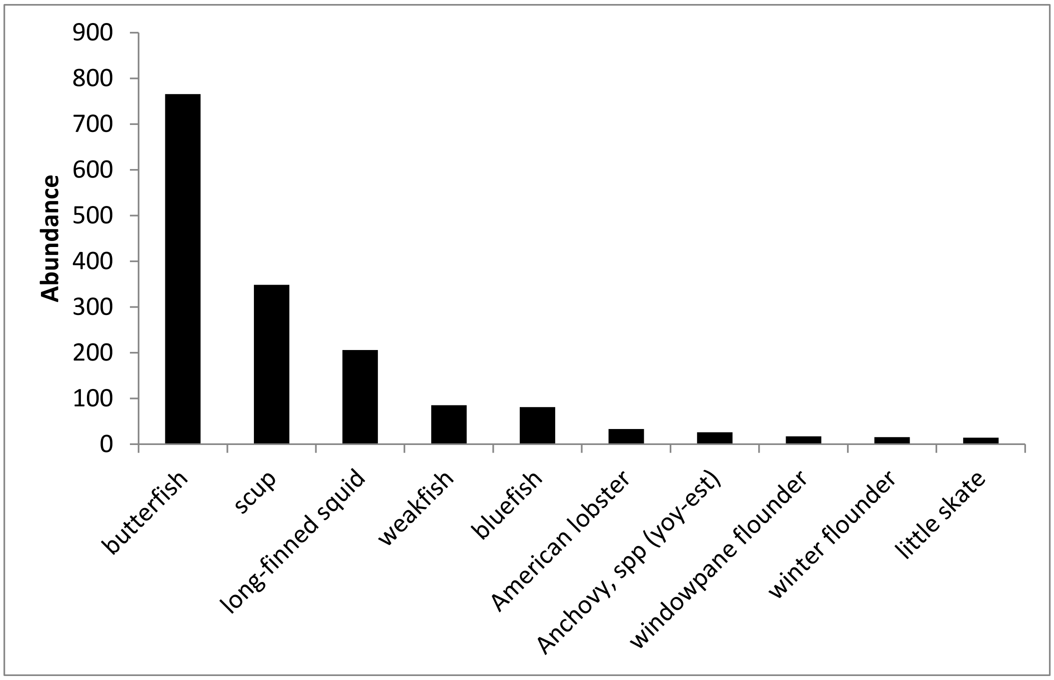


Figure 43. LIS Trawl Survey mean abundance of finfish in spring (gray) and fall (black) cruises, 1984-2008.

A.



B.

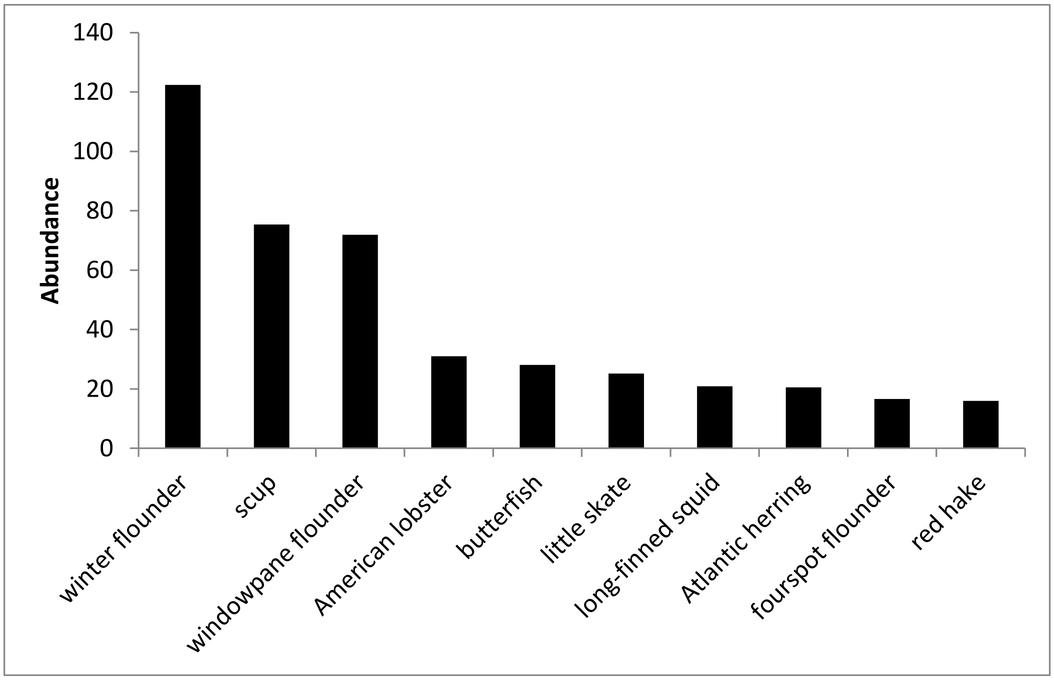
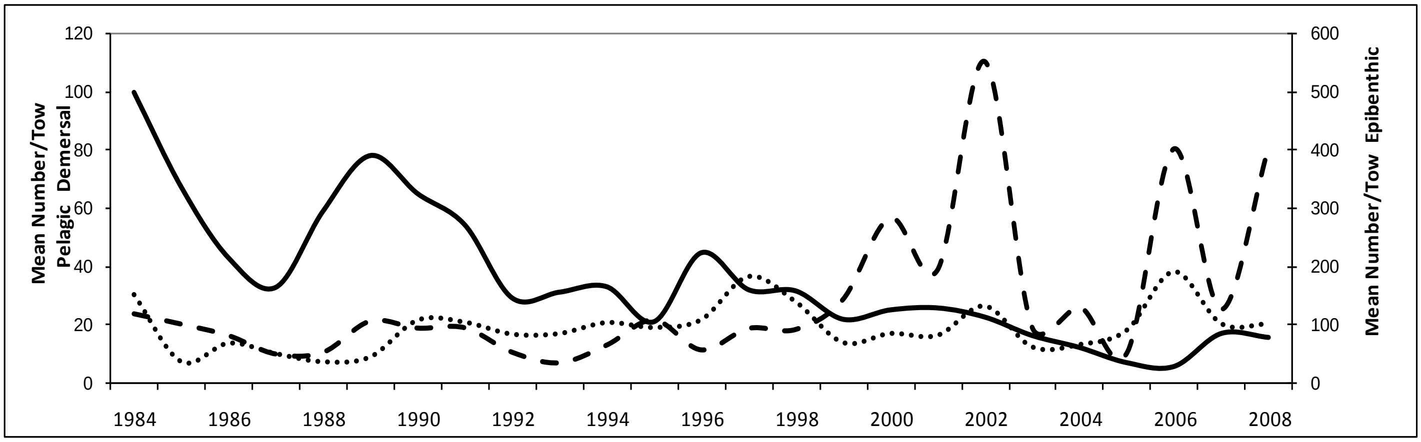


Figure 44. Top ten most abundant species captured in the fall (A) and spring (B) LIS trawl survey. Note: Of shellfish only American lobster has been reported for the duration of the survey so the relative order of the top ten species is biased towards finfish.

A.



B.

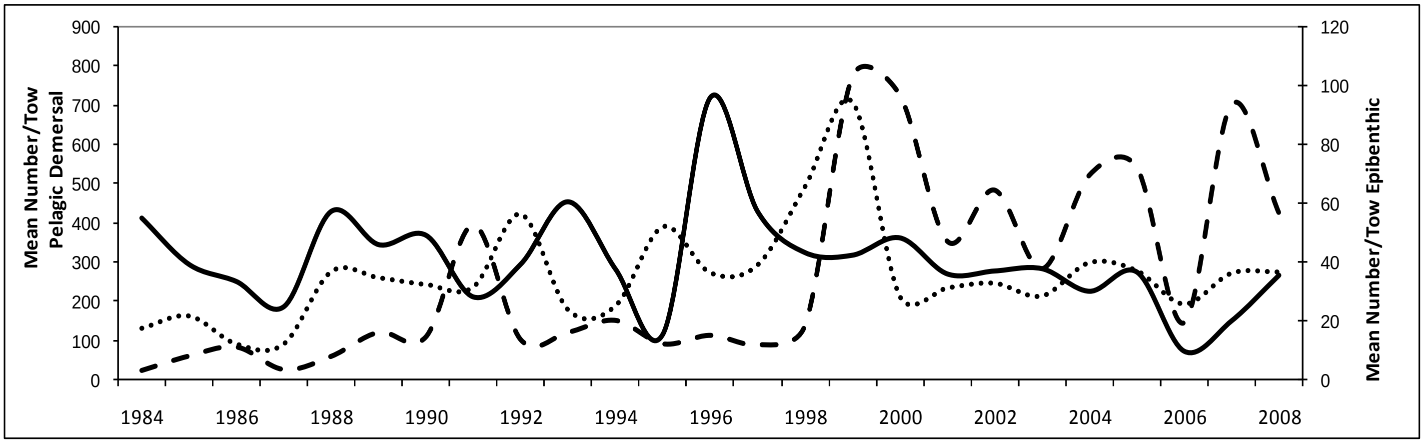
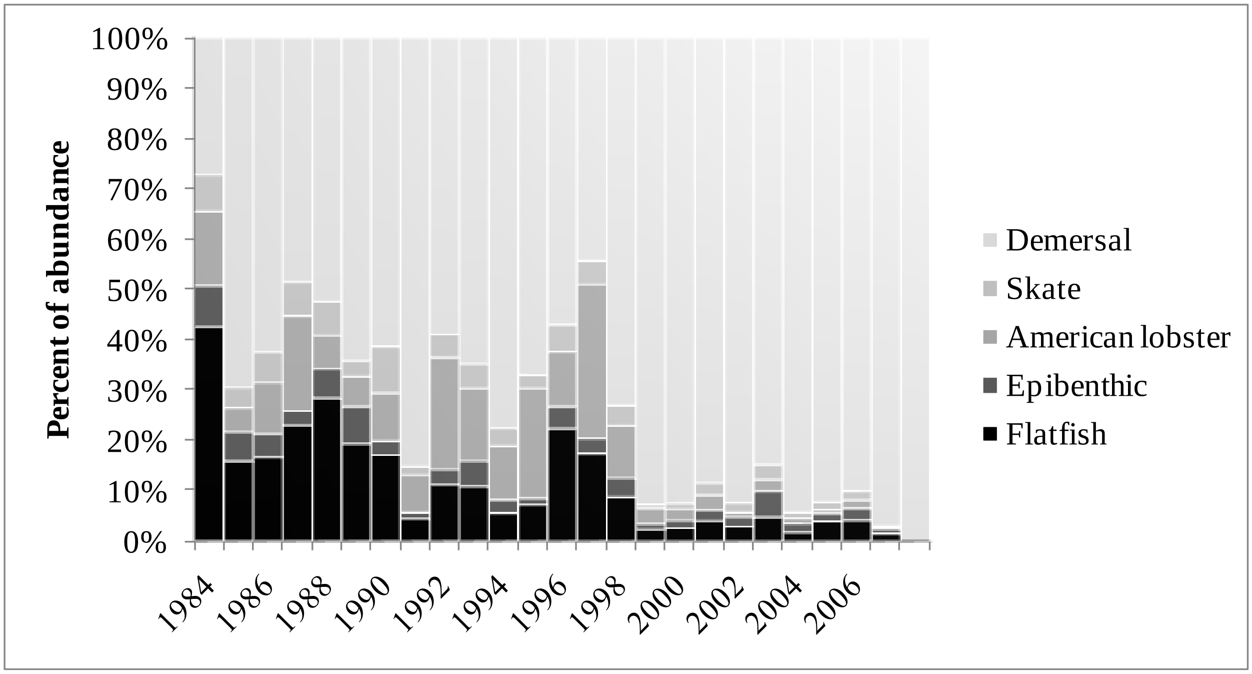


Figure 45. LIS Trawl Survey mean finfish abundance by habitat type in spring (A) and fall (B) cruises, 1984-2008. Epibenthic (solid line), demersal (dashed line), and pelagic (dotted line) species trends are shown. The negative trend in epibenthic species abundance is significant in spring (r-square = 0.67, $p < 0.001$). The positive trend in demersal species abundance is significant in spring (r-square = 0.24, p = 0.007) and fall (r-square 0.44, $p < 0.001$).

A. Fall.



B. Spring.

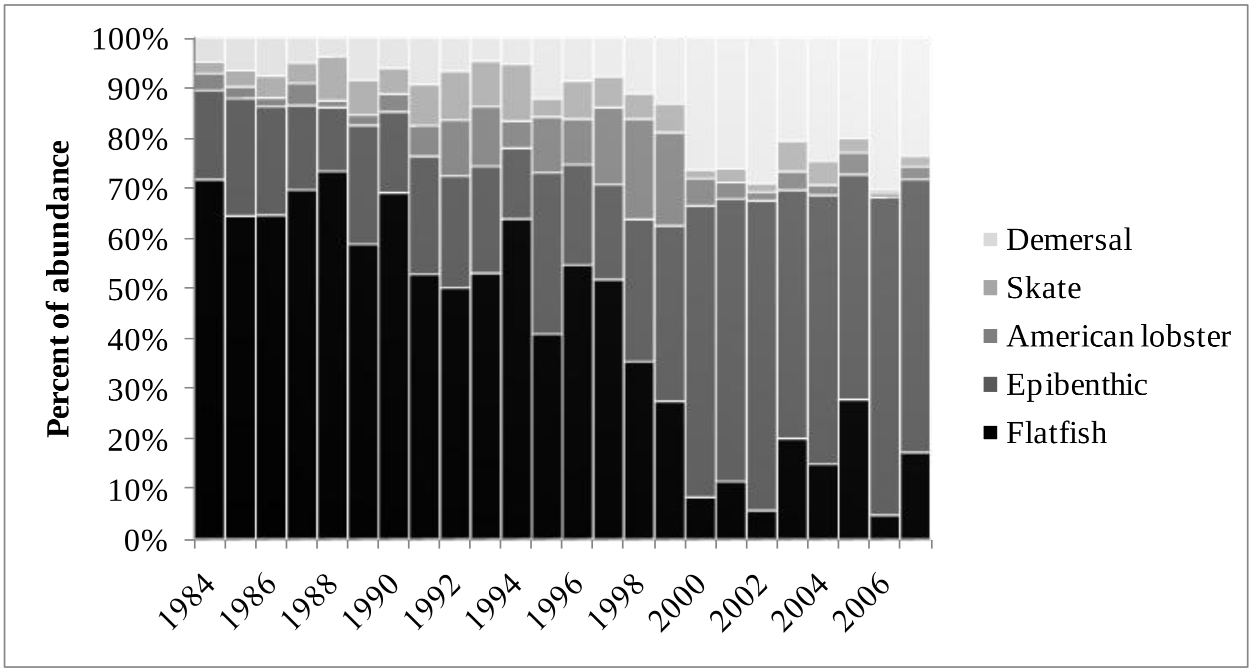
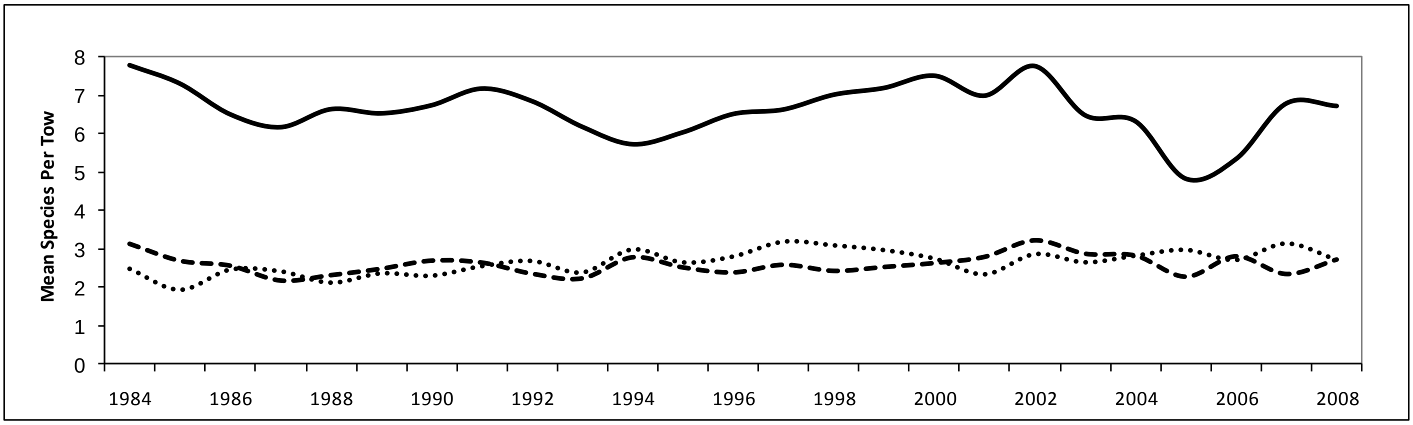


Figure 46. Trends in the percent abundance of the top 30 most abundant species captured in the LIS trawl survey grouped by demersal, skate, American lobster, epibenthic and flatfish. Note: American lobster was the only shellfish reported because it has been consistently recorded for the entire duration of the survey.

A.



B.

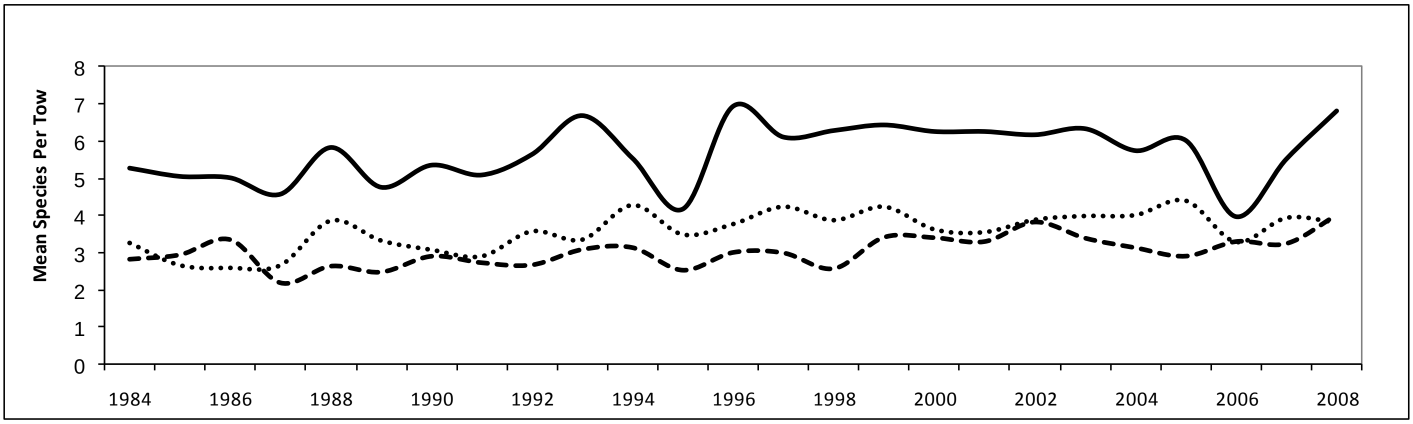
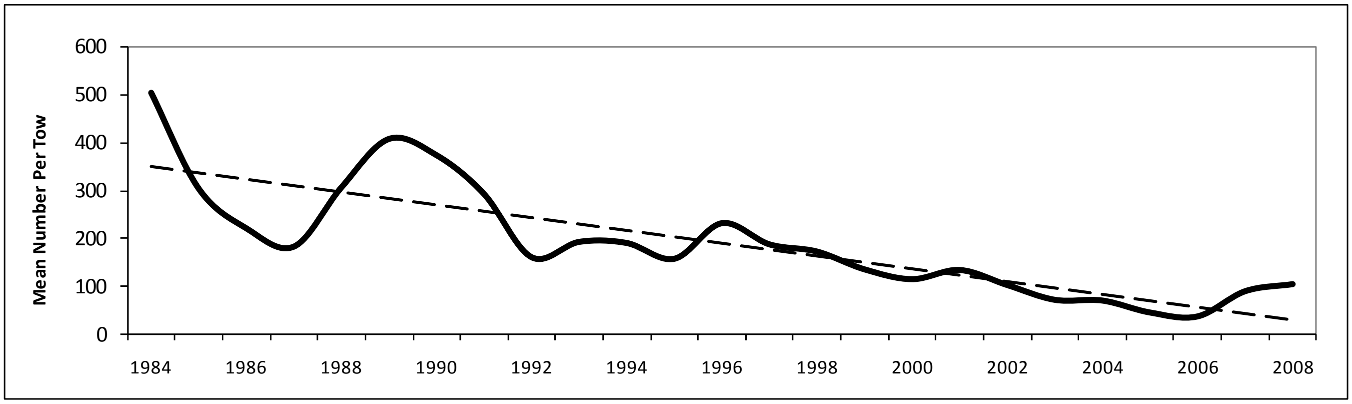


Figure 47. LIS Trawl Survey finfish diversity by habitat type in spring (A) and fall (B) cruises, 1984-2008. Epibenthic (solid line), demersal (dashed line), and pelagic (dotted line) species trends are shown.

A.



B.

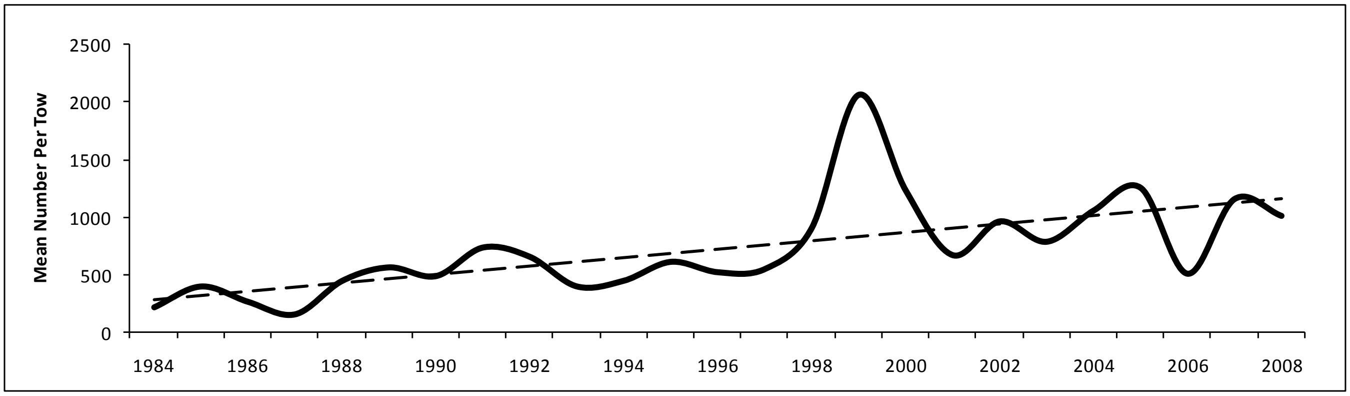


Figure 48. LIS Trawl Survey abundance of cold-adapted finfish in spring (A) and warm-adapted finfish in fall (B) cruises, 1984-2008. Significant regression slopes (dashed lines) are shown; cold-adapted r-square = 0.49 and warm-adapted r-square = 0.60; $p < 0.001$.

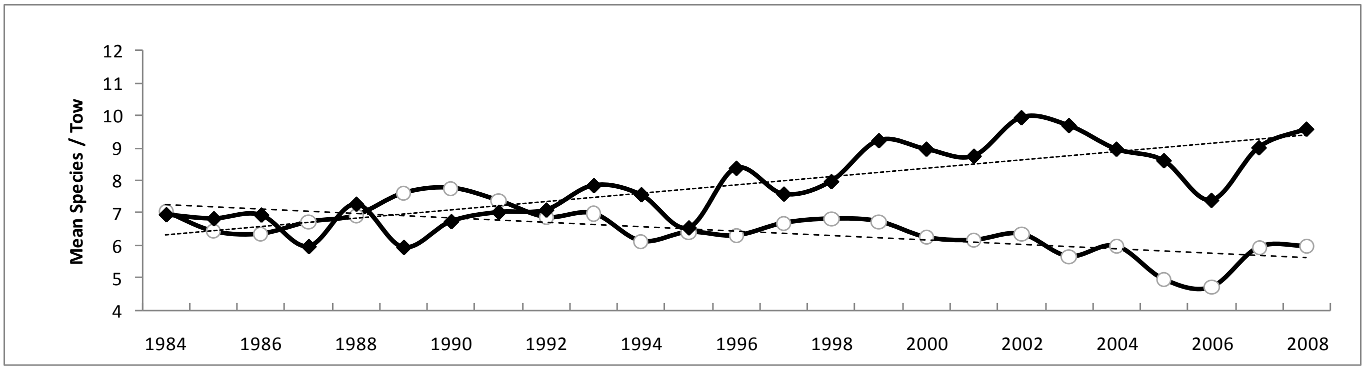


Figure 49. LIS Trawl Survey mean diversity of cold-adapted finfish in spring (open circles) and warm-adapted finfish in fall (solid diamonds), 1984-2008. Significant regression slopes (dashed lines) are shown; cold-adapted r-square = 0.49 and warm-adapted r-square = 0.60; $p < 0.001$.

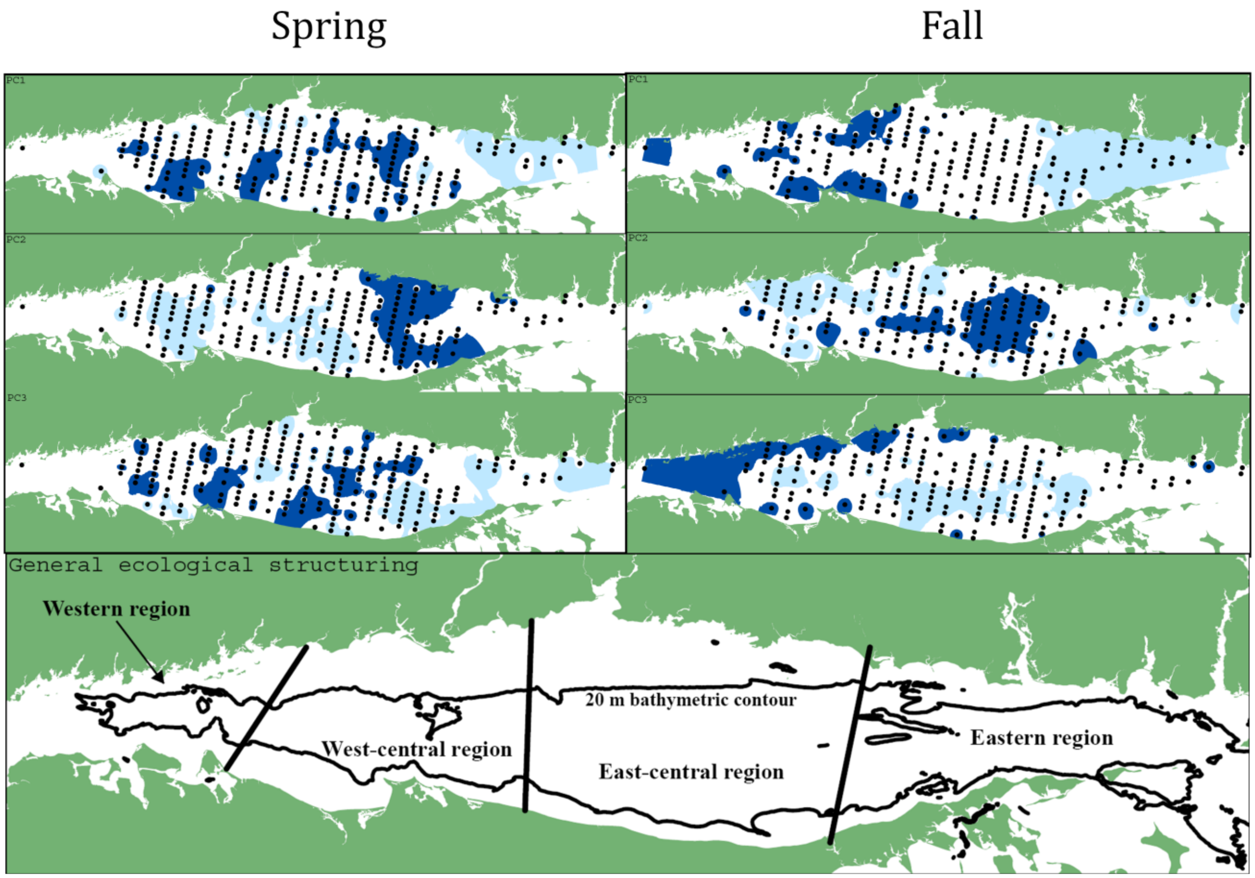


Figure 50. Results of a multivariate analysis of the Long Island Sound Trawl Survey (LISTS) data. Divisions in species groups fall along bathymetric and inner and outer Sound gradients. PCA scores for individual sites were interpolated using inverse-distance weighting; sites shaded in light had negative scores outside one standard deviation, while sites shaded in dark had positive scores outside one standard deviation. Sites with scores within one standard deviation are not shaded. Thus, species groups can be visualized as three sets (PC1, PC2 and PC3) of contrasting species groups for the spring and fall datasets. Dots represent LISTS station locations. An overall structure map is shown with bathymetry marked at the 20m contour.

Appendix 1. Definitions of the temperature adaptation and depth groups used to classify finfish species captured in Long Island Sound Trawl Survey. Classifications are based on information taken from Collette and Klein-MacPhee (2002) and Murdy et al. (1997).

ADAPTION GROUPS

Adapted to Cold Temperate Waters:

- more abundant north of Cape Cod, MA than south of New York
- behaviorally adapted to cold temperatures, including subfreezing
- preferred temperature range approximately 3-15^{0}C
- spawns at lower end of temperature tolerance

Adapted to Warm Temperate Waters:

- more abundant south of New York than north of Cape Cod, MA
- behaviorally avoids temperatures < 10^{0}C
- preferred temperature range approximately 11-22^{0}C
- spawns at higher end of temperature tolerance

Adapted to Subtropical/Tropical Waters:

- rare north of Chesapeake and occasional or rare in the mid-Atlantic
- strays captured north of mid-Atlantic are usually juveniles
- not tolerant of temperatures < 10^{0}C
- spawns only south of New York Bight

DEPTH GROUPS

Epibenthic (E)

- found exclusively or almost exclusively on the bottom
- feeds almost entirely on benthic prey
- if fished, taken only by bottom gear such as otter trawl nets

Demersal (D)

- associated with the bottom or bottom structure but may use water column occasionally
- feeds primarily on bottom organisms; uses bottom sediments in reproduction
- if fished, taken primarily by bottom tending gear or mid-water gear such as pound nets

Pelagic (P)

- uses the entire water column or primarily surface waters; eggs and larvae develop entirely in surface waters
- feeds primarily on surface prey or a mix of benthic/surface prey
- if fished, taken primarily by off-bottom or surface gear such as drift gill nets or long lines

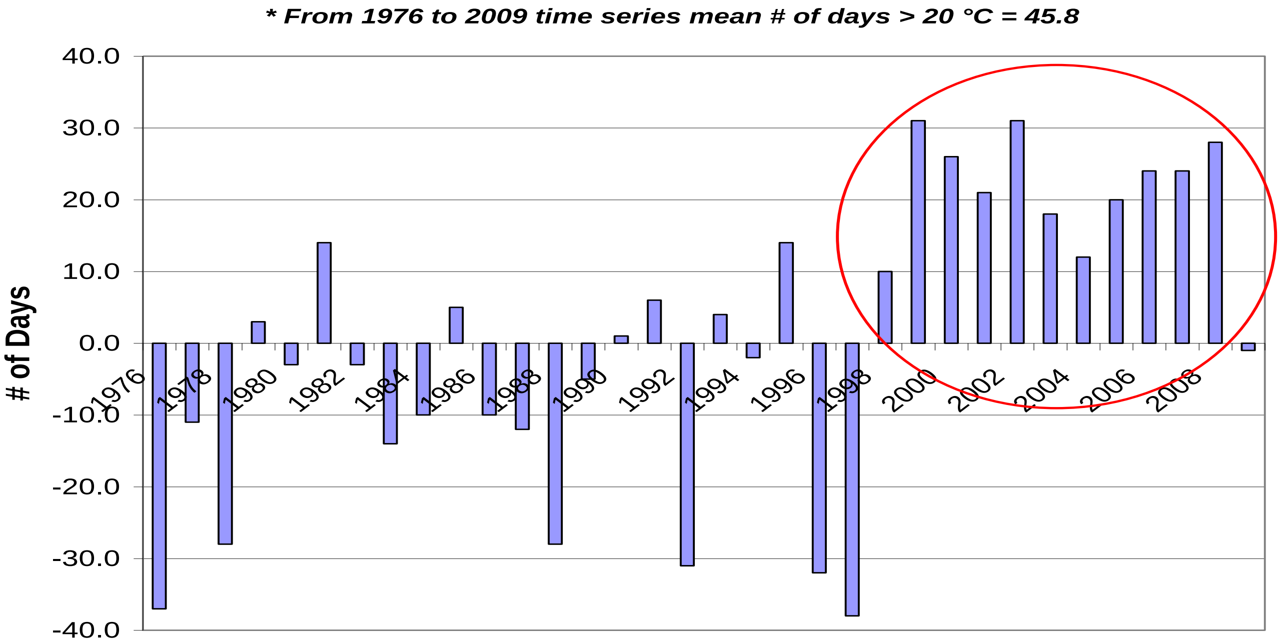


Figure 51. Anomalies from the mean number of days > 20°C of the Millstone Power Station bottom temperature, 1979 - 2009. Anomalous high values in the year since the die-off (1999-2009) are circled. Daily mean temperature is computed from continuous recordings at the Power Station intakes. Data provided courtesy of Dominion Nuclear Connecticut (DNC 2010).

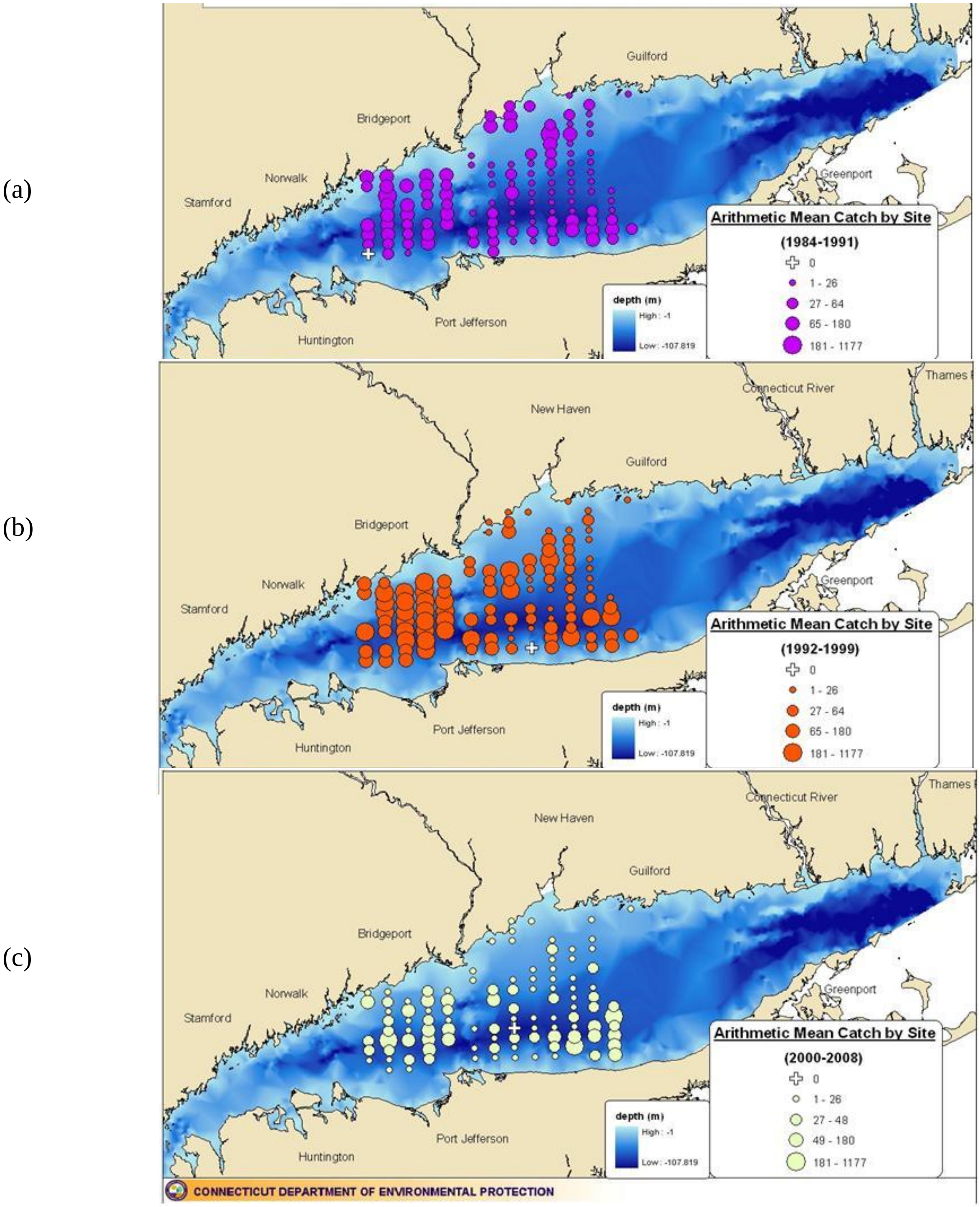


Figure 52. Special distribution was American lobster catches in the western and central basins from the Long Island Sound Trawl Survey. Arithmetic mean catches are shown for mud bottom sites only over three time periods: (a) 1984-1991, (b) 1992-1999, and (c) 2000-2008.

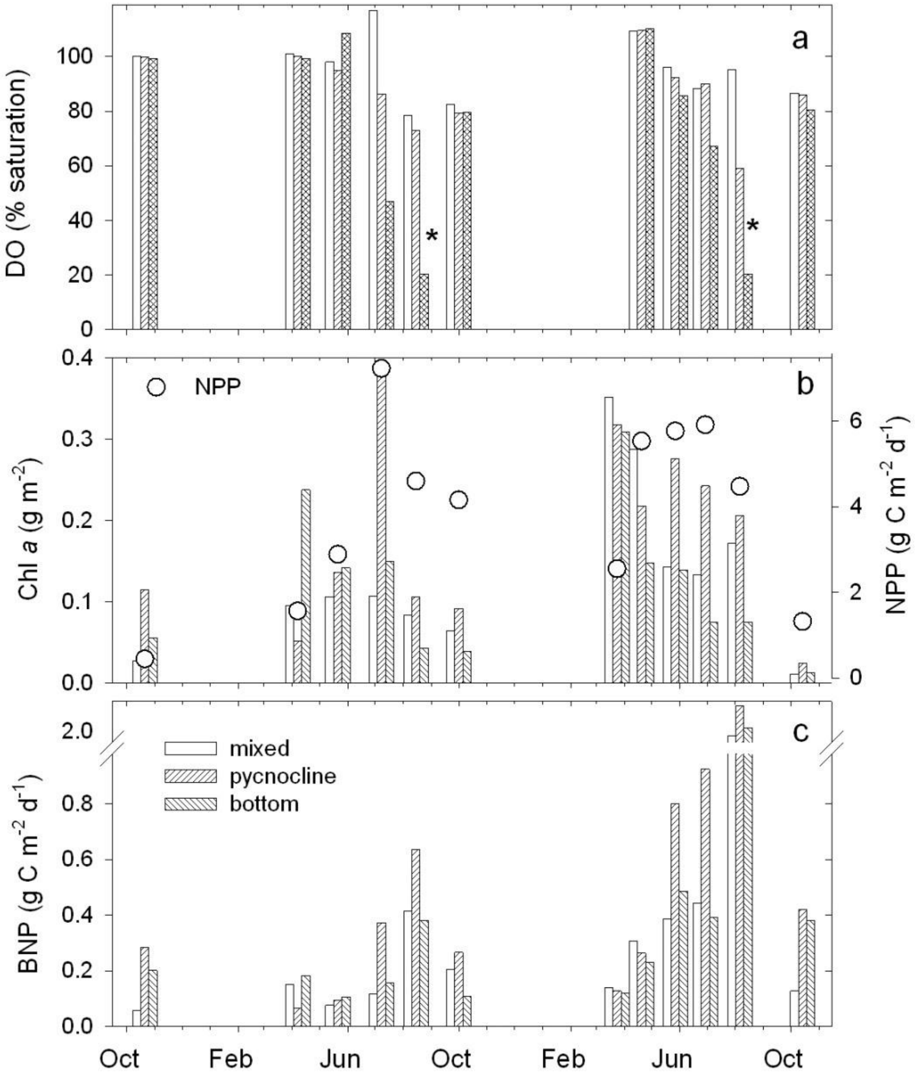


Fig. 1

Figure 53. Temporal variations in dissolved oxygen concentrations, DO (a), total chlorophyll *a* inventories, Chl*a*, and net primary production, NPP determined by ^{14}C-bicarbonate assimilation (b), and bacterial net production, BNP, determined by ^{3}H-thymidine incorporation into DNA and microscopic cell sizing (c) observed at station A4 in western LIS between 21 Oct 1996 and 14 Oct 1998. Mean DO concentrations for surface, pycnocline and bottom layers were determined from continuous profiles provided by a YSI polarographic electrode on the sampling rosette. Biomass and production measurements (b,c) were determined from discrete Niskin bottle samples collected from the middle of mixed layer, pycnocline and bottom layer and integrated over entire layer by simple trapezoidal interpolation. * = hypoxia (DO < 3.0 mg O_2 L^{-1}).

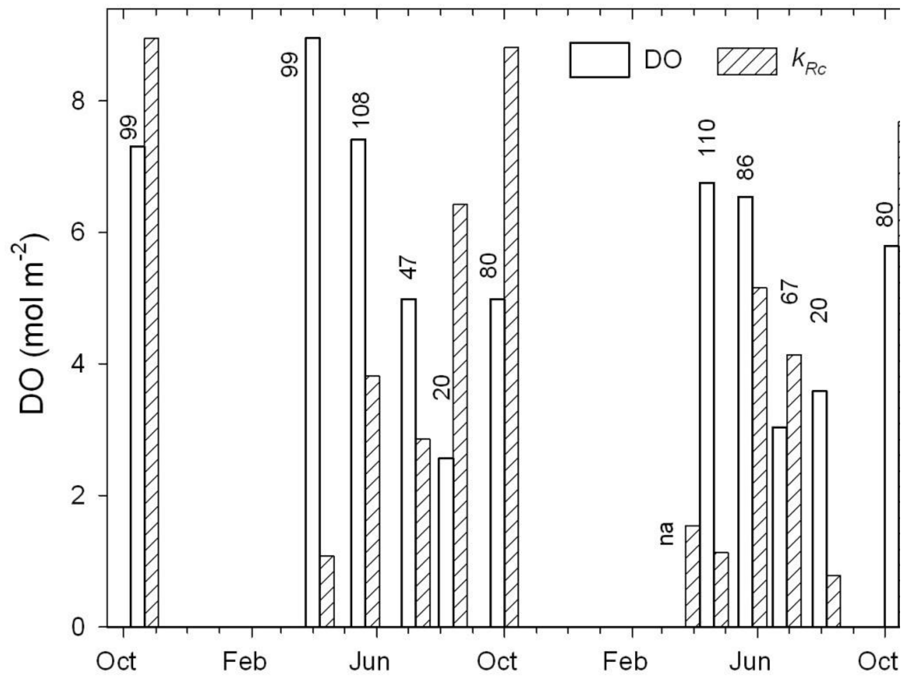


Figure 54. Dissolved oxygen inventories observed in waters underlying the mixed layer and potential respiratory turnover rates (k_{Rc}) of saturating DO levels in these waters. k_{Rc} based on community respiration rates (R_c) measured in pycnocline and bottom water samples divided by molar DO saturation calculated from temperature and salinity. Numbers above bars present observed % saturation at time of sampling.