Hydrobiologia **475/476:** 263–333, 2002.
E. Orive, M. Elliott & V.N. de Jonge (eds), Nutrients and Eutrophication in Estuaries and Coastal Waters.

The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication

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Key words: phytoplankton, zooplankton, food web, ciliates, larval fish, bacteria, protists, estuary, eutrophication, nutrients, microbes

Abstract

Current conventional wisdom argues that human-induced excesses in nutrient loadings to estuaries often stimulate 'excess' algal production leading to hypoxia, via bacterial pathways, and subsequent reduced recruitment/survival of finfish and shellfish. Why wouldn't such elevated production stimulate more animal production, rather than less? In a three-year study of Long Island Sound, U.S.A., a multitude of variables were quantified along a west to east gradient, to address the above question via the hypothesis that different successes among planktonic species experiencing eutrophication alter planktonic food web structure away from traditional pathways to microbial loop dominated ones. Variables studied included: nutrient concentrations and ratios (i.e. NO_2, NO_3, NH_4, DON, PON, PO_4, Silicate, N/P and N/Si), phytoplankton, protozooplanktonic ciliate, zooplankton, heterotrophic nanoplankton (HNAN), photosynthetic nanoplankton (PNAN), size-fractionated chlorophyll, larval fish and bacterial concentrations and/or species composition, and bacterial growth rates (as frequency of dividing cells, FDC). Results indicated that although current nitrogen and other nutrient loadings into the estuary are much higher than past inputs (especially in western waters), the average concentration of dissolved inorganic nutrients is similar (though slightly higher) to past values. Relative proportioning among chemical species does vary from west to east, with NH_4 and dissolved organic nitrogen (DON) at times more prevalent in the west, especially in bottom waters. Excess loadings of nitrogen and other nutrients into the estuary are converted to elevated biomass of both small ($< 10\ \mu$m), and large ($>20\ \mu$m) phytoplankton in the west. Slightly enhanced bacterial densities and growth rates shadow the elevated chlorophyll levels, with distinctive Sound-wide seasonal patterns that follow not total chlorophyll, but rather PNAN concentrations. HNAN concentrations also are elevated in the west, and likely influence bacterial dynamics. Species composition of phytoplankton routinely differ west to east. Inorganic N/P are routinely low (i.e. below Redfield ratios), especially in the west, while total dissolved N/P (i.e. including DON) are similar among stations and typically are significantly higher than Redfield ratios. Associated with bacterial and $<10\ \mu$m chlorophyll enhancements to an elevated diversity of ciliate species in the west. Copepod biomass is extremely enhanced in the west, indicating that while stimulating the microbial loop, eutrophication is also enhancing the secondary production preferred by larval fish and gelatinous zooplankton. Larval fish diversity is down relative to the past, but shows little contemporaneous west/east variations. So, if adult fish populations are down, but larvae are not food limited, possibly toxicity, overfishing, and/or habitat destruction which prevent a healthy, normal system response to eutrophication are culpable. It is suggested that recipients of the excess copepod production are likely gelatinous zooplankton and benthic sediments, and that unused copepod 'excess' biomass likely significantly contributes to hypoxia.

New conventional wisdom: Excess nitrogen stimulates microbial loop and net phytoplankton biomass and production, which in turn stimulates microcrustasean biomass and production and fecal release, and both significantly fuel hypoxia and likely stimulate gelatinous zooplankton production.

Introduction

Current conventional wisdom regarding many naturally mesotrophic to eutrophic estuaries argues that excess, anthropogenically introduced, nitrogen stimulates phytoplankton production, which goes underutilized, settles to the bottom of the estuary, and leads to the development of hypoxia via bacterial decomposition pathways, with concommitant decreases in recruitment and survival of commercially important finfish and shellfish (EPA Report, 1994).

Why shouldn't fertilization of these types of estuaries, and associated increases in algal biomass, over multi-year time scales, stimulate secondary & higher production leading to enhancement of finfish production rather than to hypoxia (Capriulo et al., 1993, 1997)? It is known that elevated nitrogen inputs affect plankton dynamics (Murdoch et al., 1998) and generally favor net phytoplankton over nanoplankton (Margalef, 1978; Demers et al., 1986; Kiørboe, 1993). Such phytoplankton are the preferred food of microcrustacean zooplankton, which in turn are preferred food for many larval fish. So, initially one might expect differential, time dependent growth responses of phytoplankton *versus* zooplankton, to result in increased algal biomass fluxes to the sediments, with associated elevations in microbial activity. However, eventually, over appropriate time scales, larger zooplankton, and in turn fish should respond to cyclically consistent elevated food levels with higher recruitment success and therefore enhanced populations and biomass. If eutrophication results not in enhancement of net phytoplankton, macrozooplankton and fish, but rather in stimulation of the microbial loop, it might explain widescale scientific and anecdotal reports of deteriorating finfish and shellfish stocks (Capriulo et al., 1993, 1997; EPA Report, 1994).

To attempt to address this question, we set up the hypothesis that differential successes among planktonic species experiencing eutrophic conditions is altering planktonic food web structure in the western Long Island Sound away from 'traditional pathways', and towards microbial loop dominated pathways. This study addresses several levels of questions designed to test the above hypothesis in the near shore waters of Long Island Sound, to develop contemporary baseline data on the plankton food web structure and associated nutrient dynamics of nearshore Long Island Sound waters, to search for west to east eutrophication-related gradients in microbial loop dynamics, nutrient and chlorophyll concentrations, overall water column biomass, and species composition (e.g. of phytoplankton, protozooplankton and copepods) structure , and to relate any observed differences to macrozooplankton and larval fish population dynamics. The data is here synthesized into an updated version of Riley et al.'s work of the 1950s (Riley, 1955, 1956a,b; Riley et al., 1956, 1959; Riley & Conover, 1956, 1967), expanded to cover the microbial loop, a more complete nutrient balance sheet (i.e. NO_2, NO_3, NH_4, DON, PON, PO_4, Silicate), and determination of nutrient ratios. The primary goal of this research was to describe the nearshore planktonic food web structure of Long Island Sound, and to determine if it has been changed by eutrophication. Also, if such change is evidenced, to consider whether the changes have forced the system towards a primarily microbially dominated structure, and away from a more 'traditional' macrozooplankton and larval fish structure.

Eutrophication and the question of a changed ecosystem

Eutrophication in marine systems refers to natural or artificial additions of limiting nutrients, and to the ensuing changes (Rohlich, 1969). Nitrogen is considered the primary limiting nutrient in LIS and most other coastal marine systems (Riley & Conover, 1956; Harris, 1959; Ryther & Dunstan, 1971; Mann, 1982). The prime effect of nitrogen addition on phytoplankton is an increase in primary production, but often overlooked are concommittent and related alterations of species composition and cell size distribution (Lund, 1969; Ketchum, 1969; Uye, 1994; Murdoch et al., 1998; Agawin et al., 2000).

Successful recruitment, growth and production of finfish and shellfish in aquatic ecosystems depend heavily on food quality and therefore habitat quality (Cushing, 1975; Jones, 1976; Lasker, 1981). In

particular, year classes are made or lost at the larval stages of development, with food size, quality, species composition and concentration present during larval critical growth periods determining survival rates (Lasker, 1981). For this reason, it is important to analyze and understand water column properties and dynamics that influence the structure of planktonic food webs leading to finfish and shellfish, in coastal waters and estuaries such as Long Island Sound. Anthropogenic inputs that disturb food web dynamics in Long Island Sound must therefore be identified and resultant changes in interactions understood before effective remediation can occur.

Carbon fixed by primary producers is transported along food webs through both 'copepod' and 'microbial' pathways, toward higher levels, but the proportions directed along each route depend in large part on species composition, prey quality and size (Walker & Peterson, 1991; Thingstad & Rassoulzadegan, 1999), as well as related water column chemistry and mixing dynamics. It is believed that pathways involving copepods are more beneficial to finfish populations (Greeve & Parsons, 1977; Capriulo, 1990; Capriulo et al., 1991).

The 'Microbial loop'

In recent years, it has become clear that the microbial loop (Pomeroy, 1974; Azam et al., 1983) is an integral component of most marine/estuarine food webs, and that microbial loop dynamics influence the abundance, diversity and production characteristics of fish and shellfish populations, ctenophores and crustaceans (Sherr et al., 1986; Capriulo, 1990; Capriulo et al., 1991). The term microbial loop is used to refer to planktonic (and epi) bacteria, cyanobacteria, heterotrophic (HNAN) and photosynthetic (PNAN, which includes mixotrophs) nanoplankton, dinoflagellates, ciliates and amoebae. These organisms interact intra- and inter-specifically in a number of complex ways, and are at the center of research interest and a paradigm shift with respect to our understanding of aquatic food web structure. Protistans have higher weight specific nutrient regeneration (Zeuthen, 1943; Johannes, 1964, 1965; Fenchel & Finlay, 1983; Goldman et al., 1985; Caron & Goldman, 1990) rates than do larger zooplankton (e.g. copepods) and thus dramatically influence water column chemistry (e.g. dissolved gases, nutrients, etc.) when they are present in significant concentrations (Capriulo et al., 1991; Thingstad & Rassoulzadegan, 1999). With respect to feeding, phagotrophic protists remove up to 100% of the daily bacterial production and up to 60% of the yearly primary production in different marine systems (Capriulo et al., 1991). Additionally, many protozooplankton and benthic protists can endure (and some even thrive under) exposure to 'poor water quality' (e.g. hypoxia) better than larger forms such as the metazoans, and thus will persist in 'polluted' habitats (Fenchel et al., 1990; Malvin & Wood, 1992). Despite this core of interest in the importance of the microbial loop to marine ecosystems, little research has been carried out in this area for Long Island Sound.

Microzooplankton in LIS have a community ingestion rate similar in magnitude to that of the copepod community (Capriulo & Carpenter, 1980, 1983). Microzooplankton are the main trophic link to copepods in systems where most photosynthesis is carried out by cells too small for copepods to effectively consume, e.g. coastal waters after the spring bloom (Sherr & Sherr, 1988). The microbial heterotroph sector of the food web consists of a network of bacteria and protozoa driven to a large extent by dissolved organic matter (DOM). The DOM pool is maintained via leakage of photosynthate through cell walls of algae (Larsson & Hagstrom, 1982), 'sloppy feeding' by copepods (Capriulo et al., 1988; Capriulo, 1990; Peduzzi, 1992), leaching from fecal pellets of copepods (Jumars et al., 1989), the decomposition of organic particles by bacteria using enzymatic hydrolysis (Banse, 1992), and sewage and riverine inputs to an estuary such as LIS. Releases of DOM account for 20–40% of mean primary production (Azam & Fuhrman, 1984; Hagstrøm, 1984). Bacteria feed on the DOM, and in turn are food for heterotrophic flagellates (HNANS) and ciliates (Gast, 1985). The HNANS are eaten by microzooplankton that copepods may eat (Azam et al., 1983; Ducklow, 1983; Andersen & Sorensen, 1986; McManus & Fuhrman, 1988; Capriulo, 1990; Capriulo et al., 1991; Dolan, 1991; Hoch & Kirchman, 1993). Heterotrophic microbes perform a vital function in the food web by efficiently regenerating the nitrogen in DOM to an inorganic form (Caron & Goldman, 1990; Capriulo, 1990; Thingstad & Rassoulzadegan, 1999). This function is particularly vital when limiting nutrients are all but undetectable in the spring and summer.

Bacteria

Naturally occurring planktobacterial concentrations in marine ecosystems typically range from 10^3 to 10^7

per ml, with estuaries and other coastal waters often supporting concentrations in the 10^6 per ml range (Fuhrman et al., 1980; Kirchman et al., 1982; Ducklow, 1983; Capriulo, 1990). Concentrations of bacteria in water proximal to sewage and/or storm water drainage sites often reach concentrations in the 10^9 per ml range in large part due to heightened coliform bacteria levels. It has been estimated that 10–50% of all primary production in coastal waters passes through the bacterioplankton with as much as half of that being incorporated into new bacterial biomass (Hagstrøm et al., 1979; Fuhrman & Azam, 1982). Many scientists now believe that bacteria are indispensable to the well being of many phytoplankton, which rely on various bacterial products (e.g. vitamins) for their growth.

There is now general consensus that the major consumers of suspended bacteria are small (less than 5 μm) nonpigmented (as well as some pigmented) flagellates (Haas & Webb, 1979; Fenchel, 1982; Bird & Kalff, 1986; McManus & Fuhrman, 1986; Sanders & Porter, 1988; Wikner & Hagstrøm, 1988; Sanders et al., 1992), and to a lesser extent ciliates (Børsheim, 1984; Sherr & Sherr, 1987) and dinoflagellates (Lessard & Swift, 1985). Evidence also identifies viruses as major controlling factors of bacterial populations (Proctor & Fuhrman, 1990). In sediments where bacterial concentrations are much higher than they are in the water column, ciliates and invertebrates, such as meiofaunal metazoans and polychaetes, routinely ingest large amounts of bacterial biomass (Fenchel, 1967, 1968; Capriulo, 1990).

Fate of primary production

Although micro-algal composition varies over time between net *versus* nano-sized species in many marine waters, investigations in both temperate and tropical, neritic and oceanic, waters have demonstrated that nanoplankton (and smaller) forms are often responsible for 80–99% of the observed phytoplankton productivity (Ryther, 1959; Anderson, 1965; Yentsch & Malone, 1971). Additional evidence suggests that a major portion of the chlorophyll in many marine/estuarine waters is bacterial in size (e.g. less than or near 1 μm) (Johnson & Sieburth, 1979, 1982; Morris & Glover, 1981). This production is utilized primarily by zooplankton (macro and micro forms) with microalgal size, quality and species composition determining which zooplanktonic forms predominate (Capriulo, 1990).

Tiny copepod crustaceans are the most abundant multicellular animals in the ocean water column. More than 80% of the mesozooplankton in LIS during most of the year are copepods (Deevey, 1956; Anonymous, 1976–83). As free swimming suspension feeders, they influence phytoplankton and protozoan populations (Pechnick, 1985; Lutz, 1986; Walker & Peterson, 1991). They are preyed upon in turn by larger organisms including ctenophores and fish (Deevey, 1956; Johnson, 1987; Kiørboe et al., 1988; Peterson et al., 1992; Verheye et al., 1992; Nielsen et al., 1993). Adult herring, anchovies, menhaden, and juveniles of other species that enter LIS are well adapted for feeding on copepods (Deevey, 1956). Sloppy feeding and egestion by copepods supply dissolved organic matter (DOM) and small fragments to the microbial pathway (Capriulo et al., 1988; Peduzzi, 1992), and the inorganic nitrogen copepods excrete supports primary production (Glibert et al., 1992). In addition, copepods contribute to the vertical flux of carbon by egesting rapidly sinking fecal pellets (Butler & Dam, 1994), and (or) by performing diel vertical migrations (Longhurst et al., 1990).

The broad range of water temperatures (0–25 °C) in temperate LIS induces seasonal dominance of distinct warm-water (summer–fall) and boreal (winter–spring) copepod communities, both containing species adapted to the reduced and variable salinity of estuarine waters (Deevey, 1956; Peterson, 1986). Most copepods found in LIS are also present in nearby neritic waters, but there are species present to the east in Block Island Sound that appear to be excluded by the reduced salinity of LIS. Thus the numerically important species in LIS are few: *Acartia tonsa* (summer–fall), *Acartia hudsonica* (winter–spring), *Temora longicornis* (winter–spring), *Pseudocalanus minutus* (winter–spring), *Paracalunus crassirostris* (summer–fall), *Centropages* sp, and *Oithona* sp. (summer–fall) (Deevey, 1956).

Predation upon copepods

Predation can temporarily decimate copepod populations (Johnson, 1987; Peterson et al., 1992; Verheye et al., 1992). Ctenophores can be voracious seasonal predators in LIS between the months of June and September. Copepod populations in the summer tend to vary inversely with ctenophore populations. Abundant ctenophores preyed upon the nauplii of *Paracalanus crassirostris* at a rate of approximately 25% d^{-1} in September 1985; however, in 1986, a

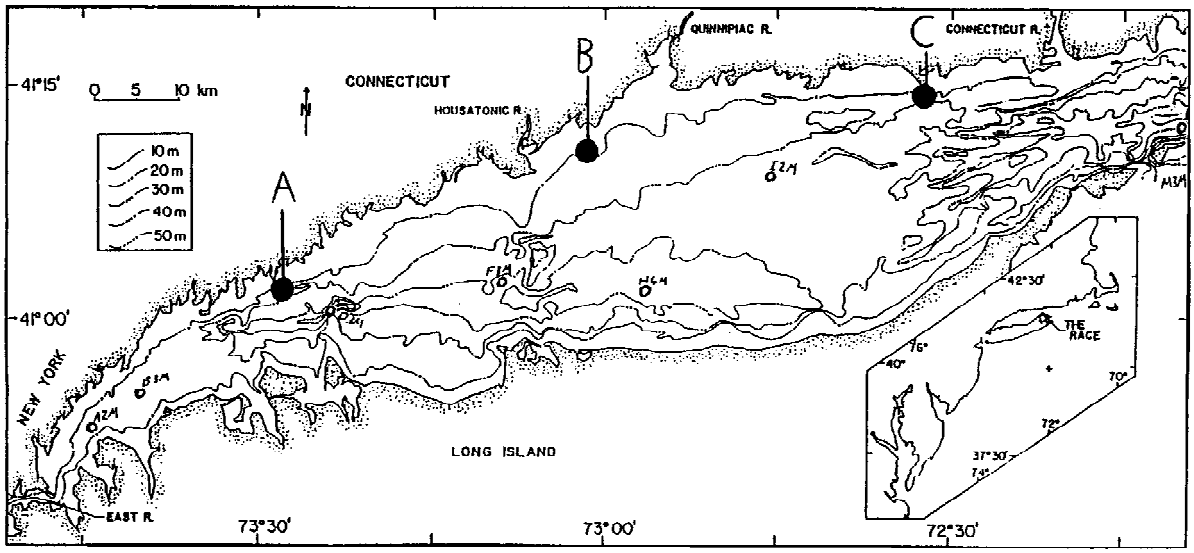


Figure 1. Map of the Long Island Sound (U.S.A.) estuary, showing the 3 study stations: A = Stamford, CT, B = Milford, CT and C = Hammonasset, CT.

year of fewer ctenophores, the nauplii of *Paracalanus crassirostris* were preyed upon by abundant *Acartia tonsa* instead (Johnson, 1987). The large predatory copepod, *Labidocera aestiva*, is never a major component of the zooplankton in LIS (Deevey, 1956; Johnson, 1987). There has been conjecture about fish limiting copepods in LIS (Peterson, 1985), and the Chesapeake Bay (Purcell et al., 1994). Anchovies, herring, and menhaden that are known to consume copepods can be quite abundant in LIS (Deevey, 1956).

Long Island Sound

Long Island Sound (LIS) is a temperate estuary with an area of about 900 nautical square miles, bordered by the states of Connecticut and New York (Fig. 1). In LIS the salinity ranges between 23 and 31 practical salinity units (PSU), the temperature ranges between 0 and 25 ° C, and the average depth is 20 m (Riley, 1955).

The most comprehensive study of the biological oceanography of Long Island Sound was carried out by a group of scientists working with Gordon Riley in the 1950s (Riley et al., 1956, 1959). This group analyzed the physical and chemical oceanography of Long Island Sound as well as the population/ecological dynamics within and among the phytoplankton, zooplankton and pelagic fish eggs and larvae. Nutrient dynamics, the role of organic matter and the biology of bottom communities were also considered. This work remains as vital to our understanding of the Long Island Sound estuary today as it was when first reported.

The Riley group estimated the annual primary fixation of carbon Sound-wide to be about 470 g cm^{-2} yr^{-1}. Of this number more than half is used in phytoplankton respiration with 205 g cm^{-2} yr^{-1} remaining available for other uses. Riley et al. further estimated that 26% of the available production goes to macrozooplankton, 31% to benthic fauna and flora and by mass balance subtraction concluded that 43% goes to microzooplankton and bacteria. The above work also reported data on phosphate, nitrate, and chlorophyll concentrations, zooplankton volume and zooplankton, phytoplankton and larval fish species composition and abundance.

Although a number of discrete studies on various aspects of Long Island Sound's biological community have been carried out over the years since Riley et al.'s work (1956, 1959), few of these have been published in the refereed scientific literature. The NOAA, National Marine Fisheries Service has conducted bacterial and phytoplankton research as they relate to shellfish ecology (Tettelbach et al., 1984; Brown et al., 1988; Wikfors in prep., Wikfors et al., in prep). These studies were generally of short duration and limited geographic range but do show clear seasonal and geo-

graphic differences in abundance and/or taxonomic composition of both bacterial and phytoplankton communities in Long Island Sound.

In the late 1970s and early 1980s Capriulo & Carpenter (1980, 1983) conducted research to examine the details of phytoplankton abundance and community structure, and tintinnid ciliate grazing on primary production in central Long Island Sound. That work found that the microzooplankton removed up to 41% of the standing crop per day, and the tintinnid ciliates 27% of the annual primary production. Also, tintinnid ciliates exhibited community ingestion rates equal in order of magnitude to the copepod community. With respect to phytoplankton, small nanoplankton often dominated microalgal communities which likely explains the success of the ciliates. The 1983 study only examined tintinnid feeding impact, yet naked oligotrichous planktonic ciliates often outnumber the loricate forms (Smetacek, 1981; Montagnes et al., 1988) in nature, and by as much as 5× in Long Island Sound (McManus, unpublished data and pers. comm; Capriulo & Pellet, unpublished data). This suggests that the actual feeding impact of ciliates is likely to be much higher than currently estimated and therefore probably is greater than that of the copepod community.

Welsh & Eller (1991) examined, physical, chemical and biological factors controlling oxygen depletion in western Long Island Sound. In the mid-1980s Peterson (1985), Peterson & Bellantoni (1987), Monteleone et al. (1987), and Peterson (unpublished data) conducted a seasonal study of the phytoplankton, copepods, larval fish and nutrient dynamics of central Long Island Sound patterned after Riley's et al. 1950s work (1956, 1959). This work ignored, as did Riley's et al. the bacterial, heterotrophic flagellate and other protozoan components of the Long Island Sound ecosystem. In fact, no comprehensive study of the microbial loop components of the Long Island Sound ecosystem has ever been carried out.

Annual plankton cycle in Long Island Sound

Distinct annual cycles in concentrations of nitrogen, chlorophyll, and copepods occur as a consequence of seasonally changing light intensity, day length, and temperature in temperate Long Island Sound. The algae are light limited in the winter (Riley, 1969). Inorganic nitrogen concentrations are high due to regeneration at the end of the previous season (Harris & Riley, 1956; Harris, 1959). As light increases, diatom blooms may be triggered by any slight increase in the stability of the water column due to the combined influences of temperature and salinity on density. Winter blooms begin as early as January, mostly in February, but can be delayed until March or later (Riley, 1969; Capriulo et al., this study). During the bloom, inorganic nitrogen decreases and particulate nitrogen increases (Harris & Riley, 1956; Harris, 1959). The bloom ends when nutrients are gone, when self-shading becomes too intense, when there is adverse weather, or when grazing becomes too intense (Riley, 1969). Copepods are generally not very abundant in winter (Deevey, 1956). A substantial proportion of the bloom settles to the bottom and decomposes, releasing inorganic nitrogen back into the water column (1956; Harris 1959; Riley & Conover, 1967; Harris & Riley, Riley, 1969).

In the spring, there are moderate pulses in phytoplankton abundance, and blooms of either diatoms or flagellates may happen in May or June if enough nitrogen is available (Riley & Conover, 1967). Flagellates begin to replace diatoms as the season progresses. Flagellates are favored over diatoms by stratification and low inorganic nitrogen (Riley & Conover, 1967; Demers et al., 1978; Margalef, 1978; Mann, 1982; Peterson, 1986; Mann & Lazier, 1991; Kiørboe, 1993). A thermocline forms at 6–8 m, usually by sometime in June (Welsh & Eller, 1991). The concentration of inorganic nitrogen becomes nearly undetectable as spring progresses, and rapid recycling of inorganic nitrogen becomes the keystone of primary production (Harris & Riley, 1956; Harris, 1959; Riley, 1969; Peterson, 1986). The winter-spring copepod species increase to their peak abundance through April and May (Deevey, 1956).

During the summer, phytoplankton populations are nutrient limited until late in the season, and remain small compared with bloom conditions; however, primary production may actually be quite high (Riley, 1956b). Dinoflagellates have largely replaced diatoms (Riley & Conover, 1956). The winter–spring copepods are replaced by summer–fall varieties, which peak in abundance around August, if not decimated by predators such as ctenophores (Deevey, 1956; Conover, 1956; Johnson, 1987). Decreasing solar radiation and water column stability late in the summer force reductions in primary production such that a surplus of nitrogen supply over utilization occurs again (Harris & Riley, 1956; Harris, 1959).

In the fall, or even as early as late August, diatom blooms can be triggered when the fall destabiliza-

tion of the water column is temporarily interrupted by some favorable combination of temperature, salinity, and light winds (Riley, 1959). Fall blooms tend to vary a lot from year-to-year, but they occasionally interrupt the autumnal increase in inorganic nitrogen concentrations (Riley, 1959). Phytoplankton remain limited by light, and dissolved inorganic nitrogen concentration peaks in November or December (Harris, 1959). The summer–fall copepods give way to winter–spring varieties in November and December (Deevey, 1956).

Estuarine copepods have been shown to feed very inefficiently on small phytoplanktonic forms when compared to planktonic ciliates offered identical food (Capriulo & Ninivaggi, 1982). Copepods exhibit higher ingestion rates when fed large *versus* smaller algae (e.g. 30 μm *versus* 10 μm nodal sizes) (Mullin, 1963; Frost, 1972; O'Connors et al., 1976, 1980). O'Connors et al., (1980) found for the Long Island Sound copepod *Temora longicornis* feeding on natural food, that maximum ingestion rates increased linearly by a factor of 3.5$\times$ as food size increased from 5 to 30 μm (i.e. flagellate to diatom dominated). Capriulo & Ninivaggi (1982) noted that the copepod/tintinnid ingestion rate ratio varied from 147:1 to 24:1 as the modal natural food size shifted from 15 μm to 4 μm, while the maximum filtration rate remained constant at about 75:1 under both conditions. These results indicate that protozooplanktonic ciliates become increasingly more important as food sizes shift towards smaller sizes. A major consequence of such a shift towards smaller algae and protozoans is a lengthening, by one or more steps, of the food chain leading from primary producers to fish. Protozoan gross growth efficiencies vary by species from a low of about 2% to a high of 82% (Caron & Goldman, 1990). These numbers suggest an average protozoan ecological transfer efficiency of approximately 30%. Thus, for each step added to the planktonic food chain by enhancement of the protozoan components of the microbial loop, a 70% reduction of resultant finfish/shellfish production can be expected. Changes in the zooplankton composition resulting from such trophodynamic shifts are important to finfish and shellfish production.

Copepods appear to feed most effectively on microplankton (plankton >10 μm) (Frost, 1972; O'Connors, 1980; Capriulo & Ninivaggi, 1982; Dam, 1989). Production within nanoplankton and picoplankton (plankton < 10 μm) may be more likely to enter the microbial pathway (Capriulo & Ninivaggi, 1982). Moreover, differences in the abundance of copepods in a food limited environment might correspond with the concentration of microplankton. The literature suggests that copepods are food limited in LIS, perhaps not all the time, and maybe not everywhere, but at least intermittently (Conover, 1956; O'Connors et al., 1980; Peterson, 1986; Dam, 1989). Copepod weight, length, abundance, species distribution, and rate processes such as growth, ingestion, excretion, and respiration vary with food availability (Frost, 1972; Conover & Huntley, 1980; Huntley & Boyd, 1984; Omori & Ikeda, 1984; Ikeda, 1985; Kiørboe et al., 1985; Berggreen et al., 1988; Cowles et al., 1988; Kiørboe, 1989; Dam & Peterson, 1991; Bautista et al., 1992; Bautista & Harris, 1992), temperature (Conover, 1956; Dam, 1989), and salinity (Deevey, 1956).

Potential altered food web structure in Long Island Sound

Several studies have shown that changes in water column chemistry (e.g. dissolved oxygen content, nutrient concentrations and relative ratios such as N/P or N/Si, presence of toxicants such as heavy meals, PCB's, DDT's etc.) alter the species composition of phytoplankton, bacteria, protozoa as well as metazoans, in nature (Thomas & Seibert, 1977; O'Connors et al., 1978; Sanders et al., 1987; Fenchel et al., 1990; Søndergaard et al., 1991). For phytoplankton, taxonomic composition, as well as gross productivity are dependent on absolute amounts and ratios of various inorganic nutrients, especially nitrogen, phosphorus, and silicate. Nitrogen and phosphorus are required by all phytoplankton, and absolute quantities of these two nutrients are generally thought to limit gross production of microalgae in marine and freshwater ecosystems (Harris, 1986). For a combination of reasons related to Molybdenum availability as well as N/P ratios, nitrogen tends to be the limiting nutrient in marine ecosystems (Howarth & Cole, 1985). Therefore, anthropogenic inputs of nitrogen stimulate algal growth in systems such as Long Island Sound. Decreasing the N input to Long Island Sound would thus be expected to reduce primary production of phytoplankton biomass. The ratio of N/P may vary from west to east because of higher sewage-derived nutrient loadings in the west. This ratio may be important in controlling the species composition of phytoplankton communities (Sakshaug et al., 1983; Søndergaard et al., 1991).

Although the absolute concentration of N is generally implicated in the limitation of gross production in

Long Island Sound, the ratio of N/Si may be the most important factor regulating taxonomic composition. Diatoms require Si for incorporation into their cell walls, to grow (Harris, 1986). The dominance of diatoms in the spring 'bloom' in Long Island Sound is well documented, as is the succession later in the season to other algal taxa, especially flagellates (Conover, 1956; Capriulo & Carpenter, 1983; Wikfors, in prep.). Research into the question of why diatoms dominate the spring phytoplankton has revealed that small diatoms possess higher nutrient uptake and growth rates than larger diatoms and other algal taxa (Geider et al., 1986; Sanders et al., 1987; Hulburt, 1988; Furnas, 1990). Replacement of diatoms by other typically small-sized algal species follows removal of the available silicate from solution by the diatoms and subsequent sinking of Si-containing cells out of the euphotic zone (Harrison et at., 1986; Anderson & Nival, 1989). Without Si, diatoms cannot sustain rapid growth rates and other phytoplankton taxa with slower growth rates become dominant, until breakdown in stratification remixes Si into the euphotic layer. A higher N/Si ratio (due to eutrophication) in western Long Island Sound should result in a shorter period of diatom dominance relative to the eastern Sound, and a longer season of flagellate dominated production in the west (Wikfors, in prep.). For reasons already discussed, this should result in reductions in regional finfish and shellfish populations and productivity.

Additionally, the 'excess' primary production stimulated by N eutrophication results in more release of algal organic exudates (Hagstrøm et al., 1979; Fuhrman & Azam, 1982) which stimulate bacterial production and therefore production of protists and bacterial grazers. Heightened bacteria and bacteria-grazer production results in lower dissolved oxygen concentrations due to high community respiration rates. Also, if the added algal biomass goes underutilized by grazers, then additional bacterial growth is stimulated via the decomposition of dead algal biomass both in the water column and the benthos. Such a result would strip more oxygen from the water column and benthos resulting in hypoxia or anoxia (Welsh & Eller, 1991). Such hypoxia/anoxia itself results in species compositional changes (Fenchel et al., 1990) superimposed on those already realized, thus further stimulating the microbial loop and driving down microcrustacean, finfish, and shellfish production.

The Connecticut Department of Environmental Protection has identified a west–east eutrophication gradient in LIS (unpublished and internal agency data). One would expect copepod stocks to respond to these gradients if eutrophication altered the amount of food available to them within the range of food limitation. Riley (1955) suggested an east-to-west increase in zooplankton in Long Island Sound; however, in a later paper, Riley (1959) implied that the data he had available did not indicate a clearly significant increase. Changes in copepod abundance, biomass, individual weight, and species have been noted to occur over gradients of eutrophication in other parts of the world (Painting et al., 1993; Uye, 1994). The switch to secondary treatment of the sewage entering LIS has shifted the form of the added nitrogen from organic forms to inorganic forms over recent decades, which may have affected the food web.

Whether nitrogen addition yields increased microphytoplankton, or increased nanophytoplankton (PNANS), is mediated by mixing, stratification, and light, as well as by the form of the nitrogen addition (Riley & Conover, 1967; Margalef, 1978; Mann, 1982; Demers et al., 1986; Peterson, 1986; Legendre & Le Fèvre, 1989; Mann & Lazier, 1991; Kiørboe, 1993). The microphytoplankton in LIS tend to be diatoms, and diatom populations are generally disfavored by stratification because they need a certain amount of turbulence to keep them mixed up into the euphotic zone. PNANS, on the other hand, are smaller and so they sink more slowly, and they may employ flagella for depth control (Demers et al., 1986; Mann & Lazier 1991). In addition, when inorganic nitrogen concentrations are high there tend to be more diatoms, and when inorganic nitrogen concentrations are low there tend to be more PNANS (Kiørboe, 1993). PNANS acquire nitrogen more efficiently than diatoms because they have a higher surface area to volume ratio, because their mobility may allow them to take better advantage of heterogenous nutrient concentrations, and because they are more likely to utilize organic nitrogen to satisfy part of their nitrogen needs (Conover, 1956; Valiela, 1984; Parsons et al., 1984; Mann & Lazier, 1991). Logically, eutrophication in LIS should favor PNANS and diatoms both over the course of the year, since conditions range from a mixed water column with high inorganic nitrogen, to a stratified water column with low inorganic nitrogen. Other factors to consider are that the euphotic zone may narrow with eutrophication due to shade produced by the additional cells (Beeton, 1969), and that a potential exists for silicon abundance to limit diatoms, but not PNANS, since diatoms require silicon to form frustules, and PNANS do not.

Changes in copepod populations tend be separated in time from changes in phytoplankton populations (Legendre & Le Fèvre, 1989; Walker & Peterson, 1991). This is because a month or more may pass before copepod populations recruit new members, whereas phytoplankton and heterotrophic microbes can double their number in hours or days (Conover, 1956; Atlas & Bartha, 1987). The implication here is that the copepod and microbial pathways partition food based not only on cell size, but also based on the match or mismatch between the temporal characteristics of food availability and those of copepod population dynamics.

Nutrient overloading has occurred in the western Long Island Sound, and hypoxic conditions in summer have been routinely encountered, particularly in the bottom waters of deeper basin sites (Long Island Sound Study Annual Report 1988, 1989/1990, and 1990) due to higher algal biomass, with maxima in the 30 μg Chl a l^{-1} or more range in the western Sound, as compared to 10 μg Chl a l^{-1} in the east (Olsen, 1975; Cosper, SUNY Stony Brook, Marine Science Research Center, unpublished data).

The fundamental question which arises from this is why the excess primary production results in hypoxia via decomposition pathways rather than enhanced secondary production of a quality leading to more fish and shellfish production. We hypothesize that the answer to this question lies in the fact that the central to western Long Island Sound food web dynamics have been shifted more towards a microbial loop dominated system as compared with the more 'traditional' food web dynamics of the central to eastern Long Island Sound. If such a fundamental shift has occurred, then both finfish and shellfish populations might be negatively affected.

Material and methods

To address our hypothesis and the major research questions of this work, the following parameters were measured at monthly intervals at three 10 meter, near shore stations (Fig. 1), on the Connecticut, U.S.A. side of Long Island Sound.

1. nutrient concentrations (ammonia, nitrate, nitrite, dissolved organic nitrogen (DON), particulate organic nitrogen (PON), phosphate and biologically active silicate), temperature, salinity and density, vertical CTD profiles and vertical oxygen profiles)
2. bacterial densities
3. bacterial growth rates (estimated as FDC)
4. total and size-fractionated chlorophyll *a* and phaeopigment concentrations (total, <10 μm, 10–20 μm, >20 μm)
5. phytoplankton concentrations and species composition
6. heterotrophic nanoplankton (HNAN) densities
7. photosynthetic nanoplankton (PNAN) densities
8. protozooplankton (chiefly ciliates) species composition
9. macrozooplankton concentrations and species composition (excluding ctenophores)
10. first approximation larval fish concentrations and species composition.

Schedule of sampling

The three stations were spaced at intervals of about 45 k along the 10 m isobath of the Connecticut shoreline, adjacent to the towns of Stamford and Milford, and Hammonasset State Park (Fig. 1). Sampling was performed monthly (occasionally weekly), typically between 0830 h and 1200 h on two consecutive days, two stations on one day and one on the next. Sampling took place for 3 years (June 1992–May 1995) at Stamford and Milford, and 2 years (June 1993 – May 1995) at Hammonasset. With an occassional rare exception 3 research vessels were used for this work: the R.V. Oceanic of the Maritime Aquarium at Norwalk, for Station A, the R.V. Shang Wheeler of NMFS, Milford for Station B, and the R.V. Libinia, UCONN Marine Science Institute for Station C. These stations are representative of the near shore western, central and eastern Long Island Sound regions, respectively.

Water sampling

Approximately 15 l of water were taken at each station from each of two depths. A model-1080 General Oceanics Go-Flow, teflon lined water sampler was used to take water from 1 m off the bottom (in a 10 m depth water column). Surface water was collected using a plastic bucket on a rope, except that water for Winkler dissolved oxygen titration was taken using the Go-Flow sampler to avoid exposure to air. Two or three casts per depth were required to obtain sufficient quantity of sample. They were combined as one sample in large Nalgene carboys. Water was dispensed from the carboy for particulate filtration, and to various bottles for a multitude of analyses. All containers, including the carboys and buckets,

were prepared by rinsing with 10% hydrochloric acid, distilled deionized water, and sample.

Physical parameters

Temperature, salinity and oxygen were measured using a combination of instruments including: a mercury thermometer, an American Optical refractometer, an Applied Microsystems STD-12 profiling unit which logged depth, temperature, salinity, and sigma-t to a computer, a YSI Model 33 SCT meter, a YSI Model 58 oxygen meter and Winkler titration (Strickland & Parsons, 1972).

Nutrient analyses

Subsamples for all nutrient analyses were transferred to acid washed, DDW rinsed BOD bottles and were placed on ice prior to same day analyses. Samples were transported from the field to the lab in an ice-filled cooler.

Nitrate, nitrite, ammonia, & phosphate determinations

Surface and bottom water nitrate, nitrite, ammonia and phosphate concentrations were determined using established, standard methods (Parsons et al., 1984). All determinations were carried out immediately after each research cruise, upon return to the laboratory. Silicate, DON and PON analyses were performed at a later date on samples that had been kept frozen (Parsons et al., 1984). Absorbences for all 3 species of dissolved inorganic nitrogen were measured using a research grade, Carey 118, spectrophotometer. Concentrations are presented as μg-at N per liter.

TDN and DON determinations

Dissolved organic carbon (DON) was measured after the method of Solorzano and Sharp as outlined in Parsons et al. (1984). Determinations were carried out in triplicate on 100-ml seawater sub-samples drawn from the original water samples, and tranferred to acid washed and distilled deionized water rinsed BOD bottles which were kept in ice filled coolers for transport back to the laboratory. All samples were pre-filtered through 0.45 μm millipore filter and kept frozen until analyses were carried out.

Total dissolved nitrogen analyses were carried out on samples collected between August 1993 and May 1995. The operational definition of TDN was that it pass a Millipore 0.45-μm membrane filter. Equipment and glass-ware contacting TDN samples were triple-rinsed with 10% hydrochloric acid prior to use. Samples for TDN were kept on ice until filtered, and then frozen in 250-ml glass Wheaton-bottles within several hours of when they were taken. Analysis was typically within a week, and performed according to method 2.1 of Parsons et al. (1984). An alkaline persulfate digestion in an autoclave oxidized all forms of nitrogen to nitrate (NO_3). The resulting NO_3 was measured according to method 1.1 from Parsons et al. (1984) by reduction to nitrite (NO_2) in a cadmium column, and the addition of color forming reagents prior to photometric determination with a Hewlett Packard spectrophotometer.

Inorganic nitrogen was also analyzed. Method 1.1 of Parsons et al. (1984) was used to determine NO_x, method 1.3 of Parsons et al. (1984) was used to determine NH_3. Ammonium was oxidized to nitrite with hypochlorite in alkali using a large excess of potassium bromide as a catalyst, and measured photometrically as in method 1.1. Dissolved inorganic nitrogen (DIN) was calculated by summing NO_x and NH_3. Dissolved organic nitrogen (DON) was calculated as the difference between TDN and DIN.

Particulate organic nitrogen (PON) determinations

Particulate organic nitrogen (PON) was measured in triplicate 100-ml seawater samples pre-filtered with 200 mesh Nitex monofilament screen. Particles were collected on 25-mm glass fiber filters with nominal retentions of 1 μm (Whatman GF/B), making the range of particle size included in PON measurements 1–200 μm. Seawater samples were transported to the laboratory on ice and filtered. Filters were stored at -80°C, wrapped in aluminum foil, until analyzed. The analytical method used for PON determinations was a heated biuret-Folin protein assay (Dorsey et al., 1977, 1978), modified according to Wikfors et al. (1984), read with a Beckman DU-40 Spectrophotometer. The use of a protein–nitrogen assay to represent total particulate N was justified based upon the assumption that non-protein PON would be very small compared with protein PON. It should be noted that PON values represent both photosynthetic and nonphotosynthetic organisms, and non-living particles within the size range selected.

Particulate nitrogen was analyzed beginning with samples from the June 1993 cruise through May 1995. PON was measured as that retained on Whatman GF/F

glass-fiber filters which capture particles nominally >0.7-μm. Filtration was typically completed within 1–1.5 h of water sampling, and filters kept on ice, until frozen at −70 °C later that day. The procedure was that of Wickfors et al. (1984) modification of Dorsey et al. (1977, 1978). Nitrogen was extracted in reagents at 100 °C for 100 min, and measured on a spectrophotometer.

Total nitrogen determinations

Total nitrogen (TN) was calculated by summing TDN and PON.

Biologically active silicate determinations

Dissolved, biologically-available silica (BSi) was analyzed in seawater samples using the molybdate colorimetric method of Strickland & Parsons (1977). The published method reports precision of ±0.14 at 10 μM; However, in our laboratory, the method was found to be linear to 0.01 μM, with accuracy of ±0.002 at 0.1 (Wikfors, unpublished data). The method was found to be non-linear, however, above 60 μM. Hence, samples containing 40+ μM BSi were diluted with deionized water and re-analyzed. Seawater samples were transported from the field on ice and frozen at −20°C until analysis within one week of collection (experiments found no significant differences in BSi values for samples analyzed immediately and those stored for up to 2 weeks at −20 °C; Wikfors, inpubl. data). Frozen samples were thawed and centrifuged at 2800 ***g*** for 20 min. prior to analysis. Extinctions were read with a Beckman DU-40 Spectrophotometer.

Phytoplankton identifications & semi-quantitative population estimates

Seawater samples for live observation were transported to the laboratory on ice. On the same or next day (usually within 2 h of collection, always within 12 h), the live samples were concentrated (about 200×) by centrifuging gently (10 min. at 1000 G) and evaluated for living phytoplankton using epi-fluorescence microscopy at 400 and 1000 magnifications. The value of observing live samples in this semi-quantitative way is that living cells could be differentiated from empty cell walls by chlorophyll *a* fluorescence in living cells. Further, photosynthetic cells less than 2 μm in size, which are virtually impossible to visualize or quantify in fixed samples, could be estimated. Percentage estimates of dominant taxa (to the lowest taxonic level possible) were made based upon the contribution of each taxon to the fluorescent particles in a few representative fields.

Phytoplankton counts

For 1994, counts were made of phytoplankton in Lugol's iodine-fixed samples from surface waters of Stamford and Hammonasset. Two liter samples were concentrated by gravity settling, through several steps, to 10–50 ml, depending upon cell density. Four subsamples of each concentrated sample were counted in an Improved Neubauer Hemocytometer (American Optical, Bright Line). Live-cell records were consulted to determine if fixed cells were likely to have been photosynthetically-active at time of collection. Counts were converted to units of cells per liter.

Chlorophyll a analyses

All water collected for chlorophyll analyses was left unscreened or was prescreened through either 10 μm or 20 μm nitex mesh and then filtered through Gelman Type A/E glass fiber filters (25 cm diameter, pore size ca. 0.5 μm). The filtration manifold was connected to a series of 2 side arm flasks, the second of which was connected to a vacuum pump set typically at 4 psi (and never above 10 psi). The apparatus was assembled for filtration of triplicate 15 ml samples each of unscreened, 10 μm mesh screened or 20 μm mesh screened water. Appropriate subtractions allowed determination of total greater than 20 μm sized, 10–20 μm sized and less than 10 μm sized chlorophyll *a* concentrations. Following filtration, filters were removed with forcepts (a necessary technique to insure that chlorophyll is not acidified via contact with hands) folded in half, wrapped in aluminum foil and placed on ice for transport to the laboratory. One and a half to 2 h after collection, samples were either fluorometrically analyzed or frozen for analysis within a few days to 2 weeks later. Each filter was removed with forcepts and placed in borosilicate glass test tubes (which were prepared with 90% grade A-19 Fisher acetone diluted with distilled deionized water) and ground up in 90% acetone using a teflon grinder attached to a variable speed drill. Glass fiber residue was removed via filtration through type A/E glass fiber filters prior to fluorometric determinations of chlorophyll using a Turner 111 fluorometer for June 1992–May 1993 samples and a Turner Designs 10-AU fluorometer for

the June 1993–May 1995 samples. Chlorophyll extract acetone solutions were diluted once more to 10 ml with 90% acetone and transferred to a cuvette. Once fluorometric measurements were recorded 2 drops of a 0.5% HCl solution were added to allow for phaeopigment determinations. This method represents a slight modification (i.e. grinding of filters for rapid chlorophyll extraction) of standard fluorometric methods (Parsons et al. method 4.3, 1984; Mantoura et al., 1990; Bidigare, 1991).

Bacterial, HNAN & PNAN analyses

Water samples for microbial analyses were collected as for nutrient, chlorophyll, phytoplankton and protozooplankton determinations. Subsamples were then transferred to a primed, graduated cylinder and 10 ml of sample were transferred to a sterile screw cap vial containing 0.5 ml of 37% formaldehyde. Two replicate vials from each depth were created and transported on ice back to the laboratory for subsequent analyses. Samples were kept at 4 degrees centigrade in the dark and typically analyzed within days to 2 weeks. An occassional sample was analyzed 4 weeks after collection.

Bacterial abundances were determined using epifluorescence microscopy and the acridine orange staining method of Hobbie et al. as described in Parsons et al. (1984). Nuclepore (0.22 μm pore size and 25 cm diameter) filters were used. Bacterial production was estimated using the FDC technique of Hagstrøm (1979) on acridine orange stained cells. Heterotrophic (HNAN) and photosynthetic (PNAN) densities were also estimated using a single filter stain technique (i.e. following the Hobbie et al. procedure for bacterial counts). The preferred method for the HNAN and PNAN determinations is a double filter (one AO stained and the other unstained) technique (Sherr et al., 1994). Subtraction of autofluorescing PNAN's on the unstained filter from the total counts on the stained filter allows for estimation of the HNAN density by difference. In a single AO stained filter technique, some HNAN's weakly fluoresce in the red range due to RNA interaction with the AO stain, giving some level of false positives for PNAN's and an underestimation of HNAN's. Due to the large quantity of parameters (most of which have time constraints related to analyses) measured on each series of sampling cruises, we could not routinely employ this double filter method. The replicate single filter AO stained samples were therefore used for approximate determinations of HNAN and PNAN densities. To determine the magnitude of potential errors resulting from this technique, we carried out the double filter procedure on a number of occassions to determine the difference in estimates gained from the 2 methods. From this a gross correction term was calculated (Table 1).

Analyses were carried out with an Olympus BH-2 Phase Contrast Epifluorescence Microscope fitted with a 100 W mercury vapor lamp, under a 100× oil plan-achromat Olympus objective. The microscope was also fitted with a whipple disk in one of the oculars, to facilitate in enumerating the bacterial cells.

While counting bacteria, those cells which were observed to be in the process of division (evident as a clear invagination of the cell wall without a distinct separatory space between cells) were noted and recorded as a percentage of the total count.

A total of four random fields were counted, and the total number of cells in each field were recorded. An additional 20 random fields were then observed, and the total number of heterotrophic (HNANs) and phototrophic (PNANs) nanoplankton were recorded. HNANs, like bacteria, because they are nonphotosynthetic and contain no chlorophyll, fluoresced bright green. HNANs were distinguished from bacterial cells by their size (roughly 2–5 times the size of bacterial cells). PNANs although typically the same size as HNANs, were clearly distinguished from HNANs and bacterial cells by the presence of chlorophyll which fluoresced bright red-orange. Flagella were sometimes clearly discernable, whereas at other times they were absent. Each cell count was then averaged together and abundance calculated. Two replicate counts were made per vial (2 vials were collected for each depth) for a total of four counts per depth and eight counts per station. Once the slides were counted, and the results recorded, the slides were placed in a microscope slide holder, labelled and placed in the freezer for reference at a later date if needed.

Protozooplankton analyses

Two liters of water from each Niskin bottle collection were fixed in Lugol's solution in a large graduated cylinder and allowed to settle by gravity for 1 or 2 weeks. Supernatant was aspirated off and samples concentrated to 100 ml. One liter from the Niskin bottle sample was fixed in Bouin's fixative (a saturated solution of picric acid in formaldehyde, with the addition of 1% final concentration glacial acetic acid), placed in a graduated cylinder and also concentrated

Table 1. Comparison of single and double filter fluorescence microscopy methods for estimating photosynthetic nanoplankton (PNAN) and heterotrophic nanoplankton (HNAN) densities, showing over and under-estimate errors and associated correction factors with respective standard deviations

PHAN density ($\times 10^4$)			HNAN density ($\times 10^3$)		
Single	Double	Corr. ×	Single	Double	Corr. ×
4.67	5.22	1.12	1.27	3.12	2.5
2.88	2.91	1.01	1.42	3.12	2.2
1.52	1.06	0.70	0.28	4.83	17.2
1.43	0.79	0.55	0.43	6.80	15.8
2.37	1.52	0.64	1.42	9.91	7.0
2.20	1.66	0.75	0.85	6.23	7.3
1.72	0.98	0.57	0.90	4.84	5.4
1.04	1.06	1.02	0.43	1.84	4.3
1.55	0.98	0.63	0.85	6.52	7.7
1.12	0.84	0.75	0.85	3.69	4.3
0.73	0.76	1.04	0.71	1.42	2.0
0.58	0.63	1.08	1.13	1.23	1.1
0.31	0.20	0.64	0.28	2.13	7.6
0.57	0.27	0.47	0.99	4.53	4.6
0.91	0.44	0.48	0.85	5.52	6.5
0.94	0.53	0.56	0.57	4.68	8.2
0.92	0.43	0.47	0.71	6.51	9.2
0.38	0.36	0.94	0.57	1.14	2.0
1.28	0.96	0.75	0.85	4.40	5.2
0.92	0.50	0.54	1.14	5.39	4.7
5.12	3.73	0.73	1.13	15.01	13.3
2.82	2.40	0.85	1.42	7.53	5.3
1.25	0.95	0.76	0.28	3.26	11.6
1.62	0.98	0.60	0.43	6.81	15.8
2.71	1.90	0.70	0.42	8.50	20.2
2.06	2.13	1.03	0.57	1.99	3.5
1.56	1.02	0.65	1.70	6.24	3.7
1.25	0.75	0.60	0.85	5.67	6.7
1.16	0.91	0.78	0.71	3.40	4.8
1.14	0.92	0.81	0.99	3.12	3.2
0.75	0.52	0.69	0.85	2.41	2.8
0.53	0.48	0.91	0.61	1.42	2.3
0.44	0.17	0.39	0.85	3.53	4.2
0.43	0.30	0.70	0.57	1.55	2.7
0.65	0.19	0.29	0.43	5.10	11.9
0.64	0.16	0.25	0.57	5.40	9.5
0.99	0.61	0.62	0.14	4.95	35.3
0.77	0.40	0.52	0.57	3.97	7.0
0.78	0.51	0.65	1.42	4.10	2.9
0.65	0.58	0.89	0.71	1.56	2.2
2.20	1.42	0.64	0.99	8.92	9.0
1.82	1.96	1.08	0.85	2.13	2.5
0.78	0.67	0.86	0.28	2.13	7.6
0.89	0.84	0.94	0.14	1.98	14.1
2.25	1.73	0.77	0.14	6.09	43.5
2.61	1.63	0.62	0.85	10.71	12.6
1.11	0.88	0.79	0.43	2.69	6.3
0.82	0.92	1.12	0.71	0.99	1.4
0.75	0.78	1.04	0.99	1.84	1.9
0.55	0.82	1.49	1.13	1.98	1.8
0.58	0.54	0.93	0.99	1.70	1.7
0.68	0.68	1.00	0.42	1.99	4.7
0.21	0.17	0.80	0.29	0.98	3.4
0.26	0.16	0.60	0.57	1.27	2.2
0.50	0.08	0.16	0.43	4.54	10.5
0.68	0.06	0.09	0.43	2.85	6.6
0.61	0.30	0.49	0.71	3.12	4.4
0.44	0.31	0.70	0.29	1.81	6.2
0.43	0.51	1.20	0.43	0.14	0.3
0.57	0.50	*0.88*	0.57	1.55	*2.7*
		AVG. = 0.74			AVG. = 7.3
		n = 60			n = 60
		SD = 0.26			SD = 7.5
		Overestimates by 35%			Underestimates by 86%

to 100 ml, as above. These samples were then Protargol silver stained (Lee et al., 1985) for detailed ciliate species identification and creation of a permanent slide collection of encountered protist species.

Macrozooplankton & larval fish ampling and analyses

Samplings for zooplankton and larval fish were carried out via quantitative, oblique plankton net tows. Two mesh sizes of 0.5 m diameter nitex nets (202 μm and 500 μm) and one 1000 μm 1 m diameter net were used. Each net was fitted with cod ends possessing windows with the same mesh sizes as the net's, as well as with two flow meters. One flowmeter was mounted within the net's brass ring mouth, the other outside the mouth of the net. This dual meter system allows for accurate estimation of the volume of water sampled (UNESCO, 1978). The 0.5 m net tows were carried out obliquely from bottom water to surface, with slow, continuous retrieval of hydrowire cable over several minutes while the ship was under way at about 1 knot. The 1 m net tow for larval fish collections was carried out by obliquely drawing the net through the water column, allowing it to fall to the bottom and again retrieving it 4 times, while under way at 3 knots.

The 202-μm mesh net was used to capture the copepods. That mesh size trapped adult copepods and advanced juveniles (copepodites), but early stages (nauplii) likely escaped due to their small size. For all

net sampling, we endeavored to maintain a constant retrieval rate, and a constant angle between the wire and sea surface in order to integrate the sample over depth. All tow-collected net cod-end contents were placed with some seawater into glass jars containing 100 ml of 10% formalin buffered with phosphate. The final concentration varied between approximately 1 and 5%.

Clogging was evaluated from the ratio of the inside flowmeter to the outside flowmeter, which provided a rough estimate of filtration efficiency. This is considered an acceptable field check, with the caveat that the outside flowmeter may be biased by water accelerating out and around the net if it begins to clog (UNESCO, 1968). An efficiency of 1.0 would imply that the net did nothing to block the flow of water. Filtration efficiencies above 0.85 are the standard set by UNESCO (1968) to assure the accuracy of volume filtered estimates.

Net tows were replicated (repeated) on thirteen occasions to test for local (intrastation) patchiness. Lloyd's (1967) index of patchiness was used to measure the intensity of patchiness, and Fisher's index was used to test for statistical significance.

Prior to examination, copepod samples were removed from their preservative with a 200-μm sieve and placed in filtered LIS water. The concentration of organisms was adjusted by appropriate use of dilution and a plankton splitter, until there were approximately 100 – 300 copepods in a 5-ml subsample of the resulting reference volume (UNESCO, 1968; Omori & Ikeda, 1984). Three 5-ml analytical subsamples were taken from the reference volume with a Stempel pipette and placed into examination dishes with raised grids (Omori & Ikeda, 1984). Examination took place on an image analysis system consisting of an Olympus Model SZHILLD 7.5 – 128 power dissecting microscope and a video system linked through an IBM type personal computer with Olympus Cue 2 software. The coefficient of variation was calculated for each set of three subsamples as a measure of counting error (Snedecor & Cochran, 1967).

Copepod biomass estimates

Copepod individual weight varies by species, temperature, nutritional history, and life stage, Due to variable animal weight loss caused by variability in the final concentration of preservative relative to retrieved sample volume, we could not use drying and weighing of the copepods as our method of estimating biomass. Biomass measurements using preserved samples can succeed only when preservative concentration and pH are kept within precise limits. If this is done, weight loss should regularly fall in the vicinity of 30% (Bøttger & Schnack, 1986). As an alternative we used published regressions of prosome length to weight for the three numerically dominant copepods, *Temora longicornis, Acartia hudsonica*, and *Acartia tonsa,* to estimate biomass. This procedure would account for the bulk of the annual population, and include the heaviest common copepod, *Temora longicornis*. Length is not changed by preservation, and can explain $\geq$94% of the weight variation found in individual samples (Durbin & Durbin, 1978; Dam, 1989). The regressions we chose gave unpreserved dry weight (UDW) as follows:

1 *Temora longicornis*: $\log(\text{UDW}) = 3.064 * \log(\text{Length}) - 7.6958$ (Klein-Breteler & Gonzalez, 1988)
2 *Acartia tonsa*: $\text{UDW} = 19.56 * \text{Length}^{3.955}$ (Durbin et al., 1983)
3 *Acartia hudsonica*: $\text{UDW} = 20.74 * \text{Length}^{3.724}$ (Durbin et al., 1992)

Length measurements were done on the image analysis system using a mouse-driven micrometer at the time that the counts were done. Fifteen individuals per species were measured in order of encounter in each of the counting subsamples, yielding 45 individual weights for each species. The average weight for each species was multiplied by its abundance to obtain its UDW biomass in units of μg m^{-3}.

Results

Physical parameters

The seasonal range of water temperatures was 0–27 °C (Figs 2 and 3). The cycle was analogous to Riley's (1956) data, and occurred in a synchronous manner at each station, except that Stamford led the other stations very slightly at times when temperature was undergoing rapid seasonal change. Transitory surface-bottom temperature gradients of 1–3 °C were noted during spring warming, but the water column was nearly isothermal for most of the summer. This suggests that the seasonal thermocline did not extend shoreward of the 10 m isobath. The water column inshore of the 10 m isobath would be expected to stay relatively mixed because of the turbulent interaction of wind and tidal energy with bottom friction

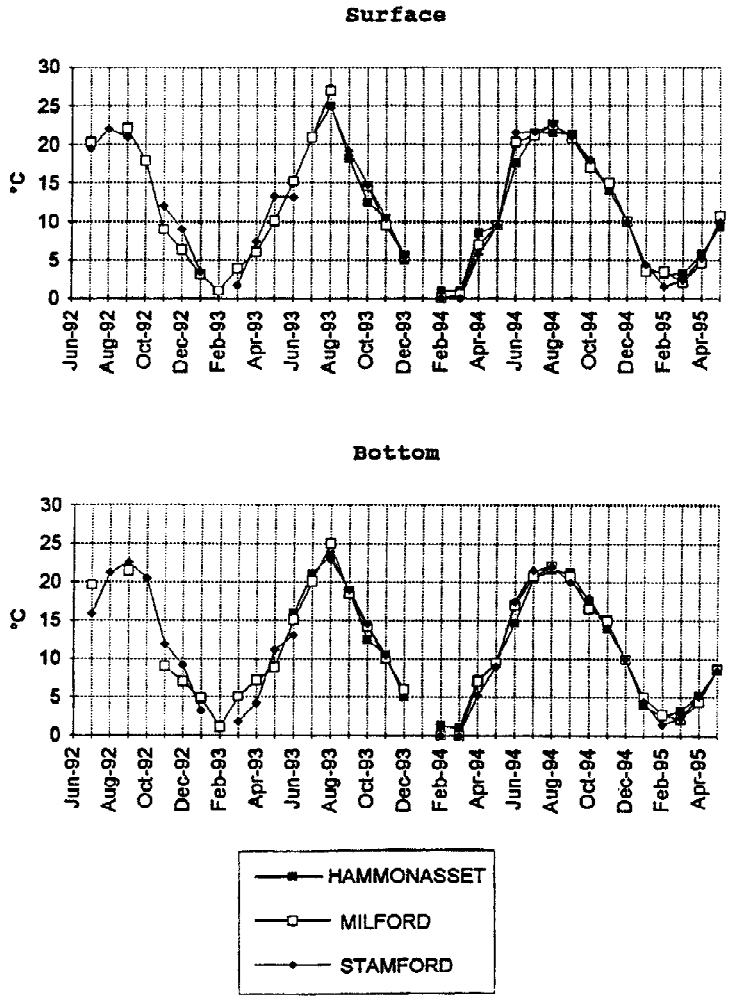


Figure 2. Annual Cycle of water temperature (°C) in the surface and bottom waters of our study sites.

and coastal features such as promontories and embayments, whereas the summer thermocline above the deep basins of LIS is typically somewhat less than 10 m deep (6–8 m) in the summer (Welsh & Eller, 1991; Johnson, 1993).

Most of the salinity data fell within 24–28 PSU, just above the center of the overall range of 20–30 PSU (Figs 4 and 5). Distinct seasonal cycles of spring lows and fall highs in salinity occurred at all stations, which Riley (1956) attributed to seasonal variation in snow-melt and run-off. The Hammonasset and Milford stations are within about thirteen and eight kilometers of river mouths, respectively, and both had broader ranges and greater variability of salinity than did Stamford. Increases between surface and bottom in average salinity were small (1–2 PSU), however, gradients over depth of several PSU occurred at times, particularly at the Hammonasset and Milford stations. There was a 1.3 PSU decrease in mean salinity between Hammonasset and Stamford, reflecting an overall east-west gradient that has been noted in LIS (Riley, 1956). The STD salinity data may have been up to 0.2 PSU in error on the low side based on a calibration of the instrument performed by the manufacturer since this study was completed.

Water column stability, as indicated by Δ sigma-t (Figs 6 and 7), depended primarily on salinity gradients rather than temperature gradients as shown by the correspondence between Δ sigma-t and Δ salinity (Fig. 6). On several occasions high values of Δ sigma-t (and Δ salinity) were noted at Hammonasset and Milford, perhaps due to their proximity to river

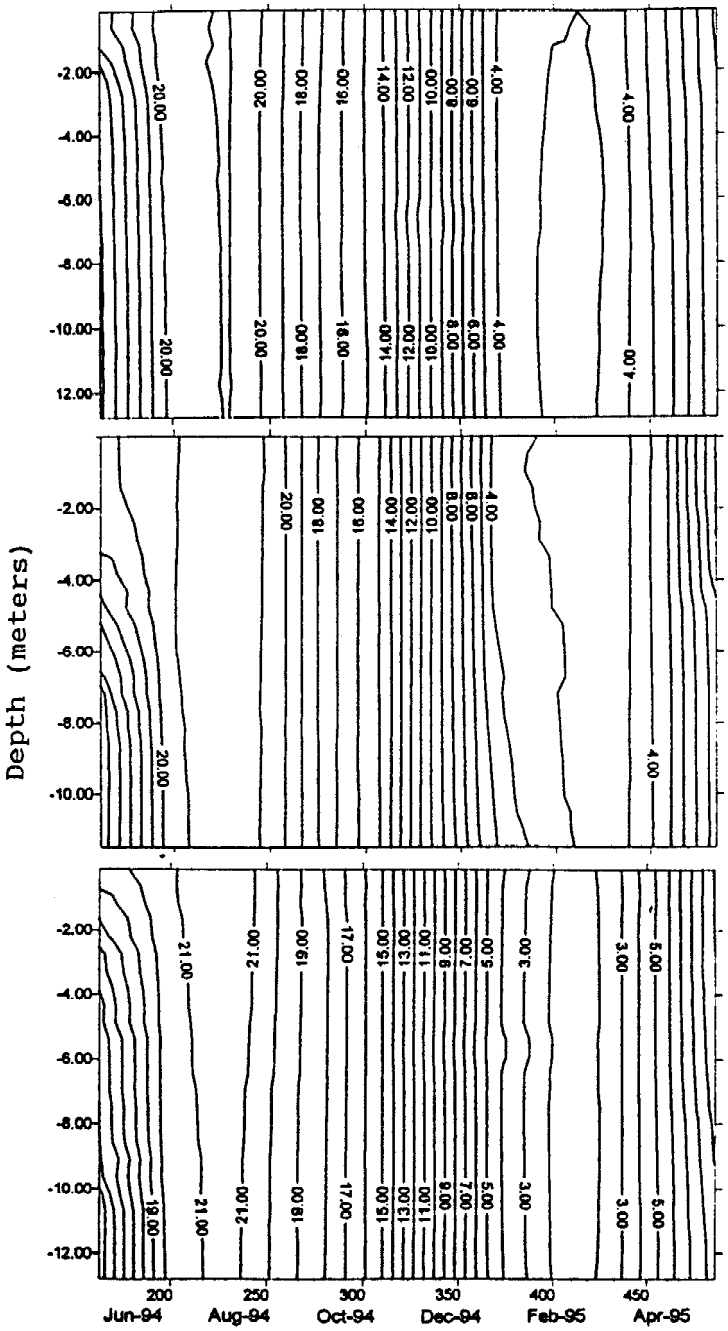


Figure 3. Vertical Contours of temperature (°C) at the Hammonasset (top), Milford (center) and Stamford (bottom) stations.

outlets. Stamford was the least variable of the three stations. All stations were stratified in June of 1993 and 1994, but they did not remain so over the summer. The water column appeared unstable (negative Δ sigma-t) on occasion, more often at Milford than at the other stations. The Δ sigma-t record obtained from STD profiles (June 1994–May 1995) was less variable than that obtained from prior measurements using a refractive salinometer and a mercury thermometer. While this difference could reflect real interyear variation, it is more than likely an artifact of the switch to the STD profiling unit. The temperature, salinity,

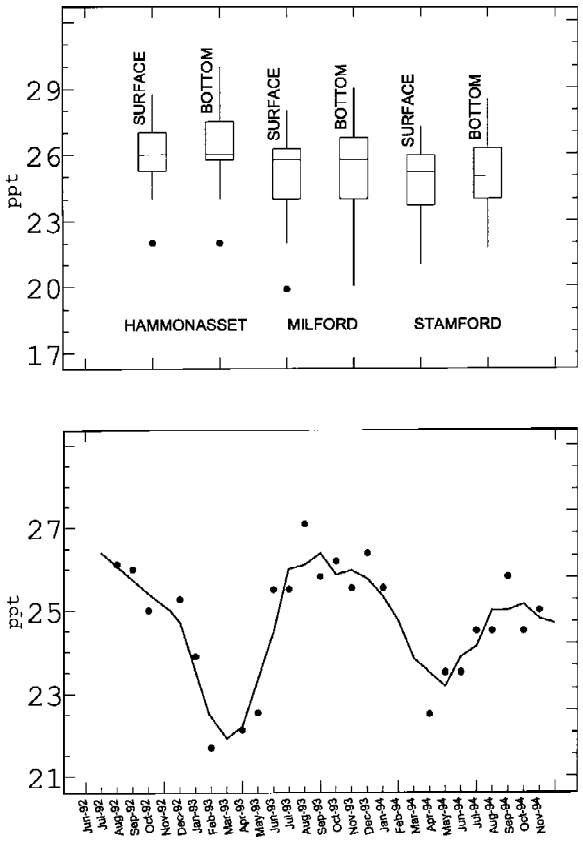


Figure 4. Box and Whisker Graph (top), shows the median salinity as a horizontal line, the central 50% of the data as a box, and the range as a vertical line. Below is an example from Stamford surface water of the seasonal salinity cycle. The solid line is a 3 point moving average. Values are in parts per thousand (PPT).

and Δ sigma-t data suggest that the mixing regime was broadly comparable among stations, but we suspect that the more frequent presence of a halocline at Hammonasset and Milford, and the westward decrease in tidal energy (Riley, 1956) probably led to differences at times.

In summary, these stations displayed similar seasonal variations of temperature, salinity, and Δ sigma-t, and were comparable to Riley's (1956) observations at near-shore stations. The Stamford station exhibited somewhat narrower ranges of salinity and Δ sigma-t than the other two stations, which are nearer large sources of riverine fresh-water. The persistent seasonal thermocline, which forms in the deeper portions of LIS, was absent.

The distribution of dissolved oxygen over depth (Fig. 8) was rather uniform and typically 80–100% saturated. There was a mild oxygen defecit during the summer and fall, which increased from east to west.

Table 2. Correlations between surface and bottom water values of nitrogen. All 3 stations were grouped for the test

Parameter	*r*	*p*	n
Total dissolved nitrogen	0.75	<0.01	57
Particulate nitrogen	0.60	<0.01	45
Nitrate+nitrite	0.97	<0.01	65
Ammonium	0.53	<0.01	65
Dissolved inorganic nitrogen	0.90	<0.01	65
Dissolved organic nitrogen	0.67	<0.01	57
Total nitrogen	0.48	<0.01	45

Bottom hypoxia was not observed at our nearshore stations, during the study period.

Nutrients

Nitrogen results are provided in nine categories: total dissolved nitrogen (TDN), particulate nitrogen (PN), nitrate, nitrite, nitrate+nitrite (NO_x), ammonium (NH_3), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), and total nitrogen (TN) (Figs 9–18). Strong seasonal cycles in NO_x and DIN were concurrent in the horizontal (east–west) axis and the vertical (surface–bottom) axis. Changes in the other nitrogen parameters, although not always so synchronized, generally shared the same seasonal time frame at each station and depth. Surface and bottom concentration values were significantly correlated with one another in all categories (Table 2). Station-to-station differences were clearest when concentrations were above average, and less clear, or perhaps too small to detect, when concentrations were below average.

Dissolved inorganic nitrogen (NO_3, NO_2, NH_4)

Nitrate

When chemical species were considered individually, Milford waters were found to have higher average nitrate concentrations than Hammonasset waters, and concentrations in Stamford waters were higher than those of both Milford and Hammonasset (Table 3). As expected, nitrate levels were fall/winter seasonally highest. As was true for the physical parameters, bottom and surface water nitrate profiles were similar to each other at all 3 stations. Nitrate patterns and highs were similar to those observed by Riley et al. in the 1950s for their near shore stations. Additionally, significant and meaningfull year to year variability was observed in nitrate patterns at our stations (Fig. 9).

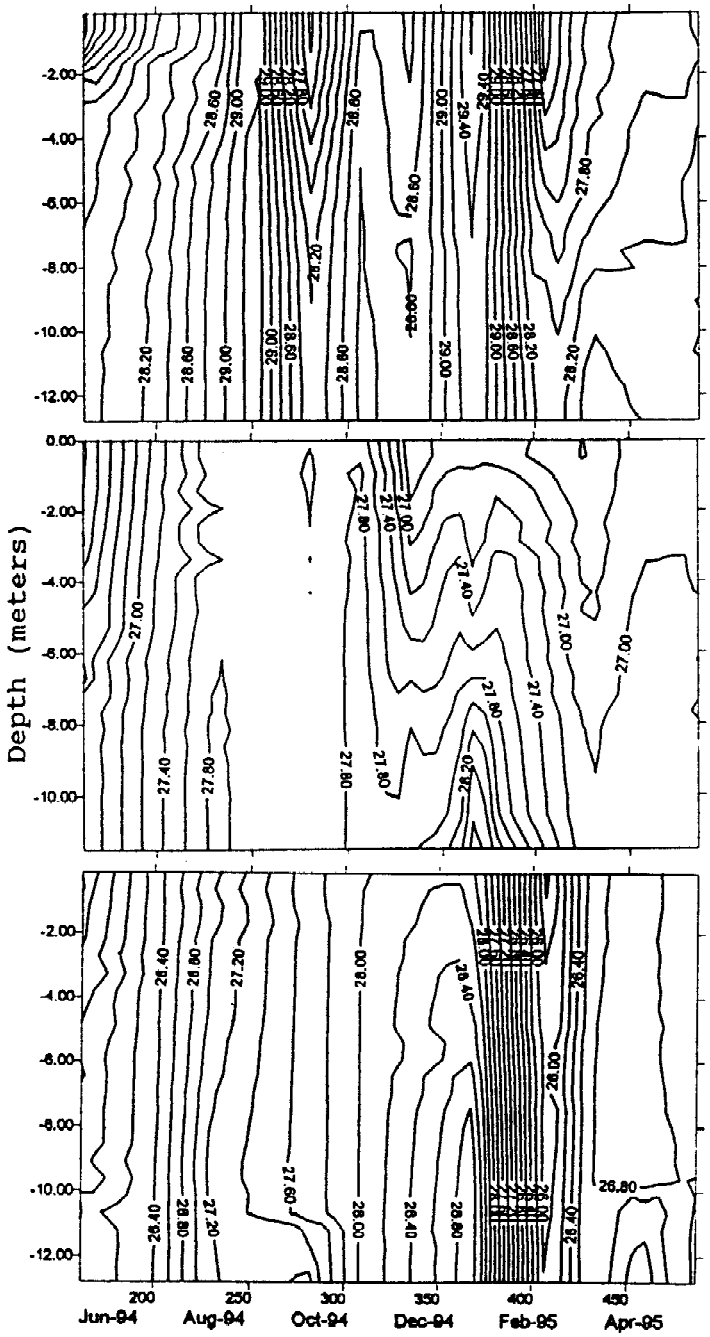


Figure 5. Vertical Contours of salinity (Parts per thousand, PPT) at the Hammonasset (top), Milford (middle) and Stamford (bottom) station.

Nitrite

Nitrite levels were consistently low (mostly in the 1 μg-atm range with occassional highs of 4 μg-atm, Figs 9 and 10) with minor peaks corresponding to highs in the nitrate fall/winter concentrations.

Ammonium

The range of NH_4 concentrations was from the detection limit ($\sim$0.1 μM) to 10 μM (Figs 9 and 10). Ammonium ion concentrations (after the normal seasonal variations were accounted for) were far more variable than nitrate and nitrite levels, although, over-

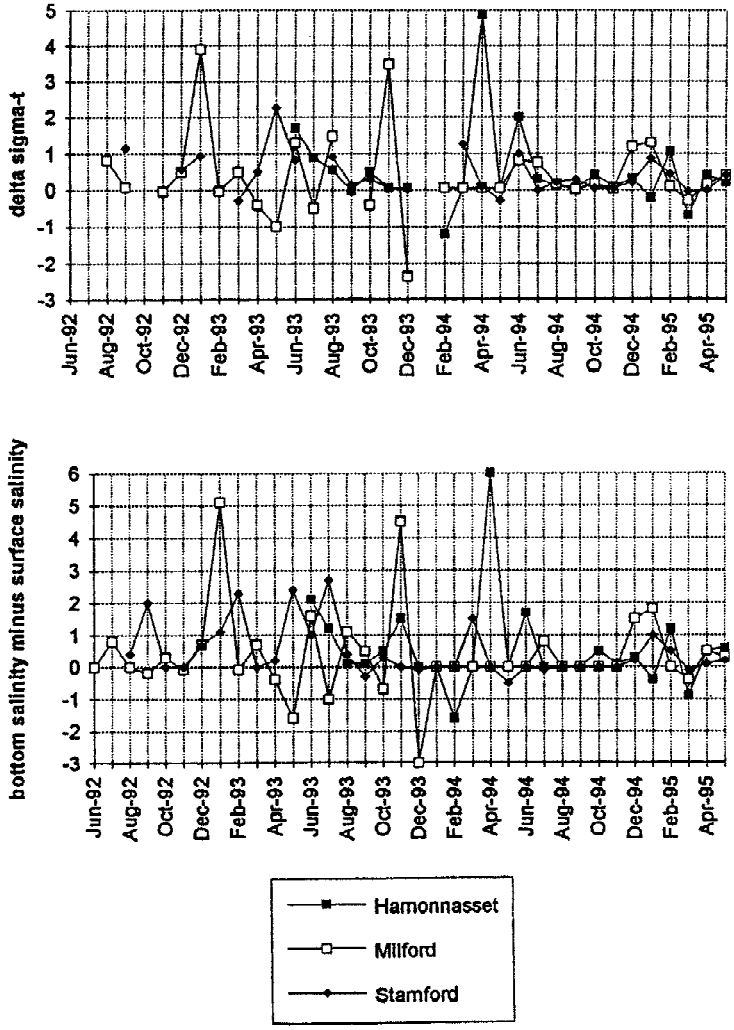


Figure 6. Water column stability expressed in sigma T density units, or (kg/m^3) -1000 (top) and bottom salinity minus surface salinity in PPT (bottom).

all they tended to follow NO_x patterns. Seasonal trends at the different stations seemed to be out of phase with each other from June 1992 until April 1993. The pattern between stations in 1994 and 1995 was more coherent. Values tended to be above average in August 1993, December 1993, April 1994, and August–September 1994. No one station had consistently lowest NH_3, and station-to-station differences produced no overall trend in mean concentration at the surface over the period of study. Bottom water concentrations were higher than surface levels likely due to the influences of microbial and animal metabolic activities. At the bottom, concentrations decreased between Hammonasset and Milford, and increased between Milford and Stamford, with Stamford highest overall (Table 3). Stamford waters exhibited greater differences and higher peaks than the other 2 stations. The mean NH_3 concentration in bottom water was higher than at the surface (Table 3), and there were strong contrasts between surface and bottom some months (note June-September 1993 at Stamford).

Nitrate + Nitrite

The range of NO_x concentrations was from below the detection limit ($\sim$0.1 μM) to 28 μM (Fig. 11). There was an obvious seasonal-cycle with values above average from September or October until February or March, and below average from February or March until August or September. In fall 1992, NO_x was more abundant than in fall of the two following years,

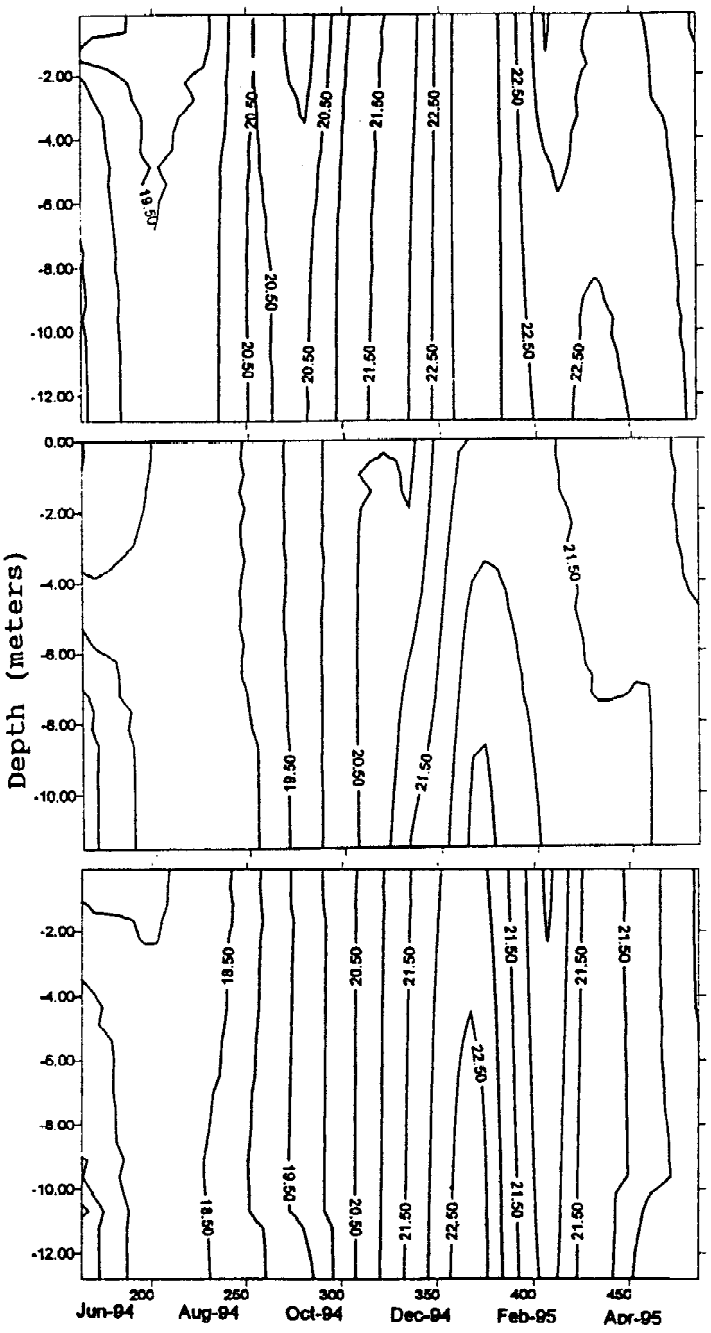


Figure 7. Vertical Contours of density expressed in sigma T units, or (kg/m^3) −1000 at Hammonasset (top), Milford (middle) and Stamford (bottom) stations.

which opposes the year-to-year pattern in Chl. No one station had lowest NO_x at all times, but Hammonasset was usually lowest during the fall-winter peak. Moreover, station-to-station differences were consistent enough to produce modest east–west trends of increase in mean concentration over the period of study (Table 4). Average surface concentrations increased between Milford and Stamford, and bottom concentrations increased between all three stations. The mean concentration was slightly higher at the

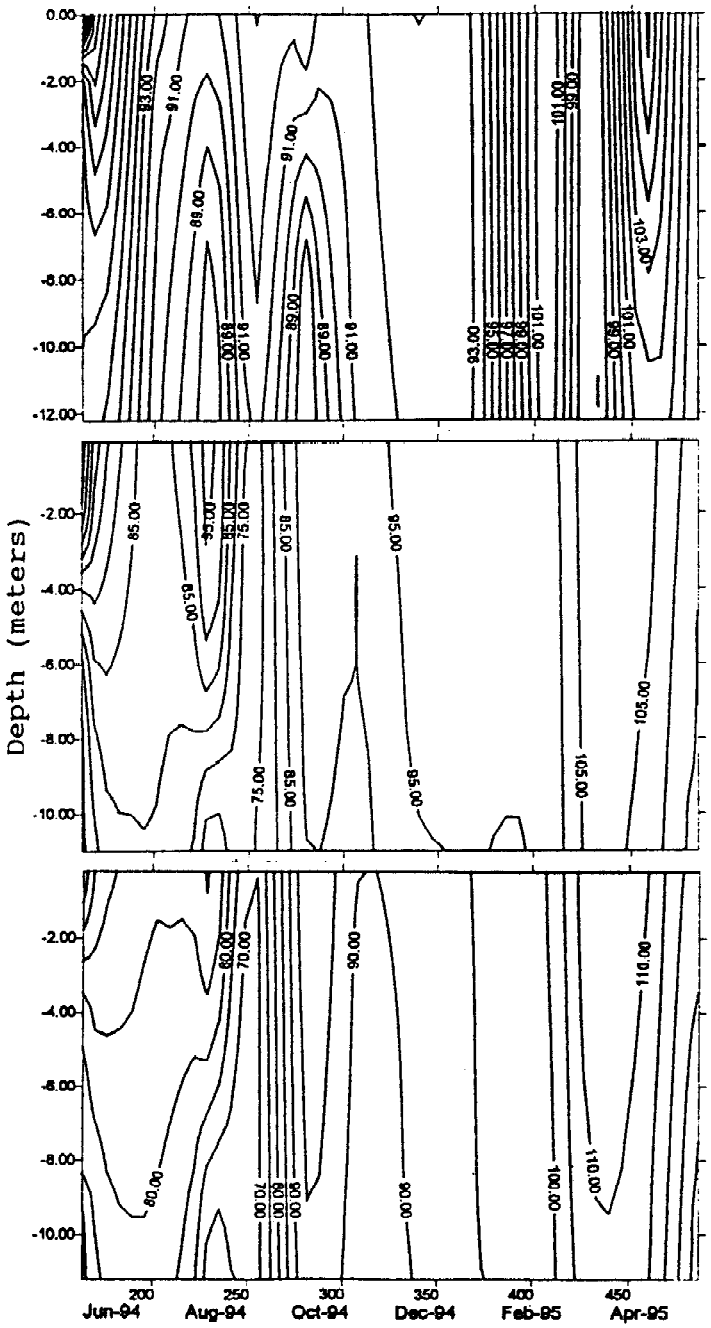


Figure 8. Vertical Contours of dissolved oxygen in units of % saturation, at the Hammonasset (top), Milford (middle) and Stamford (bottom) stations.

surface at Hammonasset, and slightly higher at the bottom at Milford and Stamford (Table 4).

Dissolved inorganic nitrogen

The range of DIN (NO_x plus NH_3) concentrations was from 0.13 μM to 29 μM (Fig. 12). On average, most (75%) of DIN was in the form of NO_x, thus the strong positive correlation between temporal variation in DIN and NO_x (Tables 3 and 4) is largely autocorrelation. Concentrations were high from September until February, and low from March through August. There was a clear pattern with Hammonasset lowest when DIN

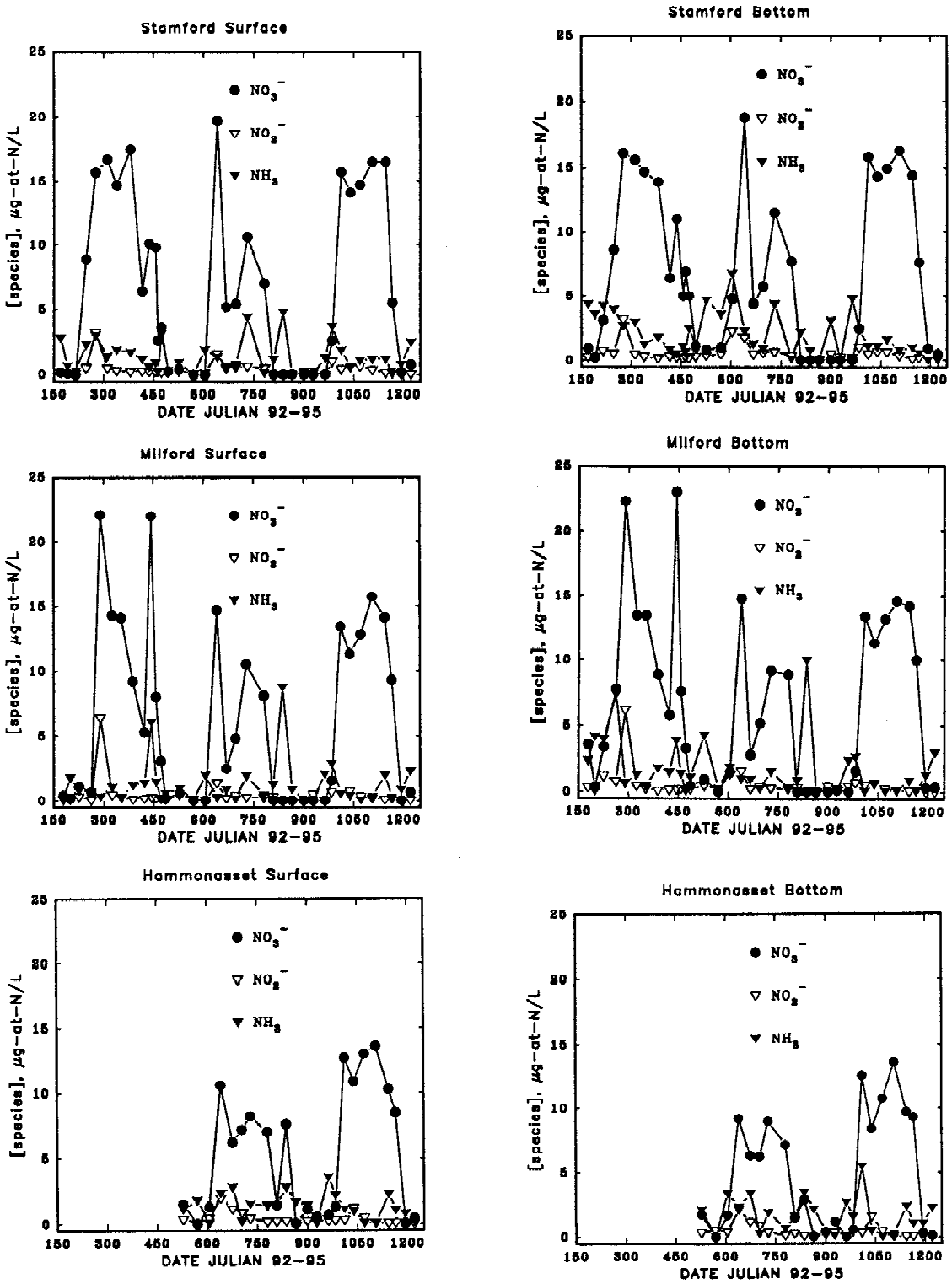


Figure 9. Concentrations of nitrate, nitrite and ammonia in surface and bottom waters over the course of this study. Dates are presented as Julian values beginning January 1, 1992.

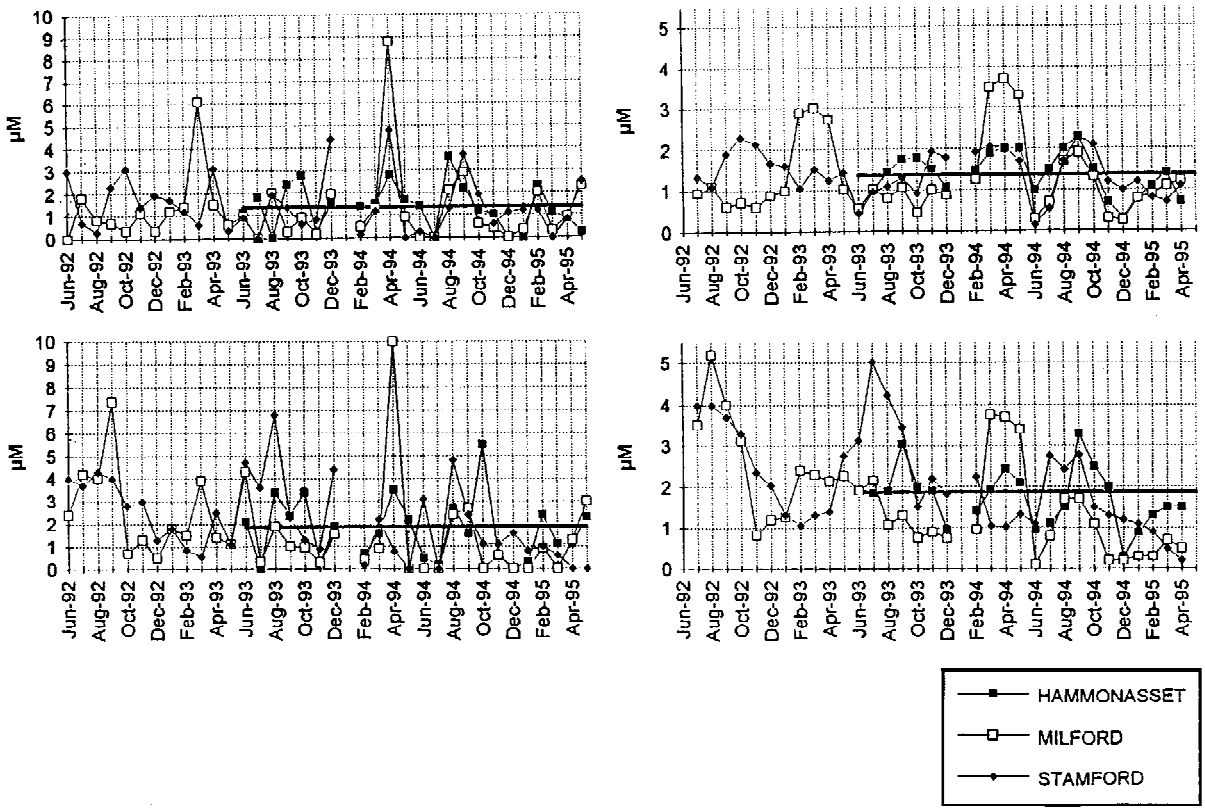


Figure 10. Ammonia concentrations in surface (above) and bottom (below) waters of the 3 study sites. On the right, data are presented as 3 point running averages. The straight lines are the composte means for the 3 stations for the 2 year period when all 3 stations were sampled.

was high in the fall and winter of 1994–1995. No one station had consistently lowest DIN, and station-to-station differences produced no overall trends in mean concentration over the study period between Hammonasset and Milford. Stamford, however, exhibited a small but consistently higher TIN level at the surface, and a larger one at the bottom (Tables 3 and 4). The overall mean for bottom water was slightly greater than for surface water at Milford and Stamford, but not at Hammonasset (Tables 3 and 4).

Total dissolved nitrogen

The range of concentrations of total dissolved nitrogen was 7.6 – 40.2-μM (Fig.13). TDN was commonly above average from September until February, and below average from April until August. No one station had lowest TDN all the time, but Hammonasset often did (Fig. 13), and these station-to-station differences were consistent enough to produce modest east-west trends of increase in mean concentration over the period of study (Table 4). The increase occurred between Hammonasset and Milford at the surface, and between all three stations at the bottom. The TDN mean was slightly higher at the surface than at the bottom at each of the stations (Table 4).

Dissolved organic nitrogen

The range of DON (TDN minus DIN) concentrations was from 0.8 to 28.2 μM (Fig. 14) however, only one value was below 4.4 μM (September 1993 at Hammonasset). Temporal variation was often (but not always) coherent between stations and between depths, and the patterns were not as distinct or regular as for DIN. Values were below average in March and April 1994, and again for an extended period from November 1994 through April 1995. Values were above average in October and November 1993, and again in June and July 1994. The October–November high of 1993 was not repeated in 1994. No one station had consistently lowest DON, but station-to-station differences were consistent enough to produce modest overall trends in mean concentration over the period

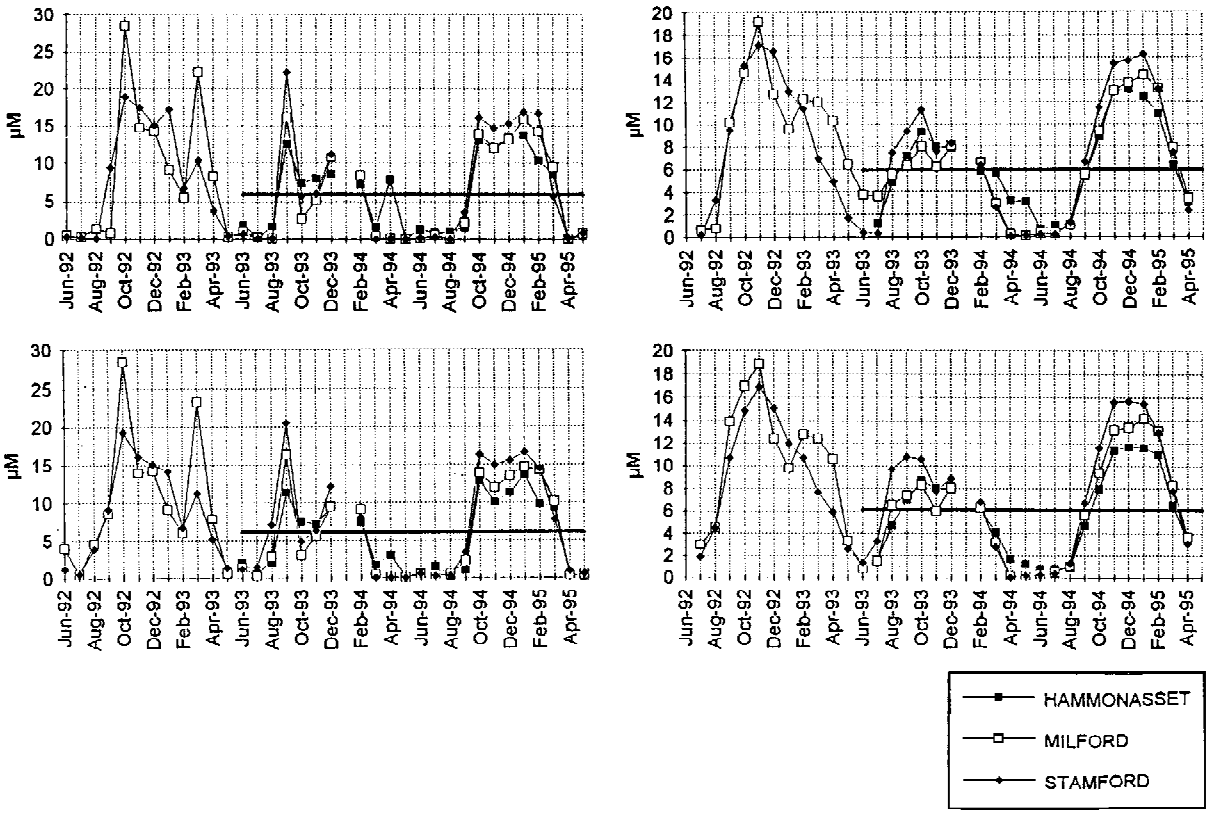


Figure 11. Nitrate and nitrite (NO_x) concentrations in the surface (above) and bottom (below) at the 3 study sites. See Figure 10 for data presentation details.

of study (Table 4). On average, there was an increase between Hammonasset and Milford at the surface, and small east–west increases between all three stations at the bottom. There were differences between surface and bottom at times, but with no clear pattern. Overall, there was slightly less DON in bottom-water relative to the surface (Table 4).

Particulate organic nitrogen

Particulate organic nitrogen (PON) at the three sites varied generally between 2 and 42 μM, but only one measurement (August 1994 at Hammonasset) exceeded 28 μM (Figs 15–17). Seasonal cycles in PON are not pronounced, although slight increases in early spring and late summer may be discerned. With the exception of a peak in Hammonasset during August, 1994, large accumulation of nitrogen in standing stocks of suspended microbial biomass does not appear to be occurring. PON, summed for the entire study, is only slightly higher in Stamford than in Milford and Hammonassett; the difference is not statistically significant (ANOVA $p>0.05$). Peaks of PON corresponded with phytoplankton blooms that took place in August, October, and March. There were tendencies for PON to be below average when TDN was above average, from October to December, for example in 1994. No one station had consistently lowest PON, and station-to-station differences were consistent enough to produce only small east–west trends of increase in mean concentration over the period of study (Table 4). These small increases occurred between all three stations at the surface, and between Milford and Stamford at the bottom. There were sometimes distinct differences between surface and bottom, coincident with surface-bottom chlorophyll differences: bottom-PON exceeded surface-PON in March 1994, and vice-versa in August 1994. There was an overall tendency for PON in bottom waters to be slightly higher than at the surface (Table 4).

It should be noted that PON represents N contained in photosynthetic and heterotrophic microorganisms, as well as non-living particles. Factors limiting accumulation of PON include nutrient uptake

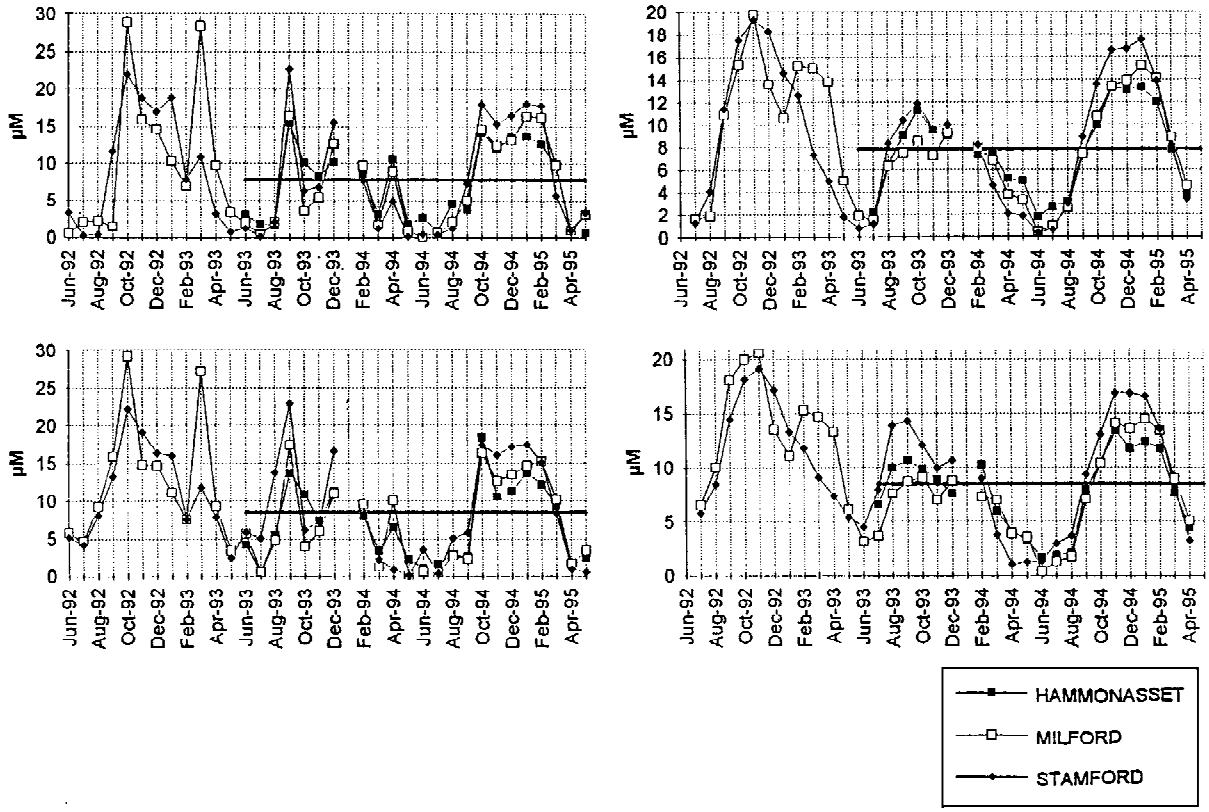


Figure 12. Dissolved inorganic nitrogen (DIN) concentrations in the surface (above) and bottom (below) waters of the 3 study sites. See Figure 10 for data presentation details.

by microplankton, consumption of microplankton by meioplankton, and sinking, either as whole cells or as fecal pellets. Some evidence that sinking was an important sink for PON during this study is found in consistently higher PON values in bottom samples than in surface, when values are averaged for the entire study (Fig. 18). Interestingly, differences between surface and bottom PON values are more pronounced in Hammonasset and Stamford than in Milford. Microscopic observations suggest that PON in Hammonasset bottom samples may be accounted for to a large extent by benthic diatoms; whereas, bottom-water PON in Stamford is likely dominated by zooplankton fecal pellets.

Total nitrogen

The range of TN (TDN plus PON) concentrations was from 17.1 to 61.5 μM (Fig. 18), but only one value exceeded 50 μM (August 1994 at Hammonasset). Temporal patterns consisted of decreases and below average values from February until May in 1994, and above average values from September until November in 1993 and in July and August in 1994. No one station had continually lowest TN, and station-to-station differences were consistent enough to produce only small trends in mean concentration over the period of study (Table 4). On average, there was an increase between Hammonasset and Milford at the surface, and an increase between Milford and Stamford at the bottom. Differences between depths were obvious at certain times (note fall 1993 at Milford, and August 1994 at Hammonasset).

Nitrogen summary

The distribution of nitrogen compounds varied seasonally; the proportion of DIN in TN ranged below 1% during spring and summer, to as high as 60% during fall and winter; the proportion of DON in TN ranged around 50–60% in summer and fall, but could drop in winter to 30–40%; the proportion of PN in TN averaged 35%, but ranged as high as 70% during blooms. These seasonal variations took place in a more-or-less concurrent manner at each station, consistent with the behavior expected of nitrogen in a temperate estuary

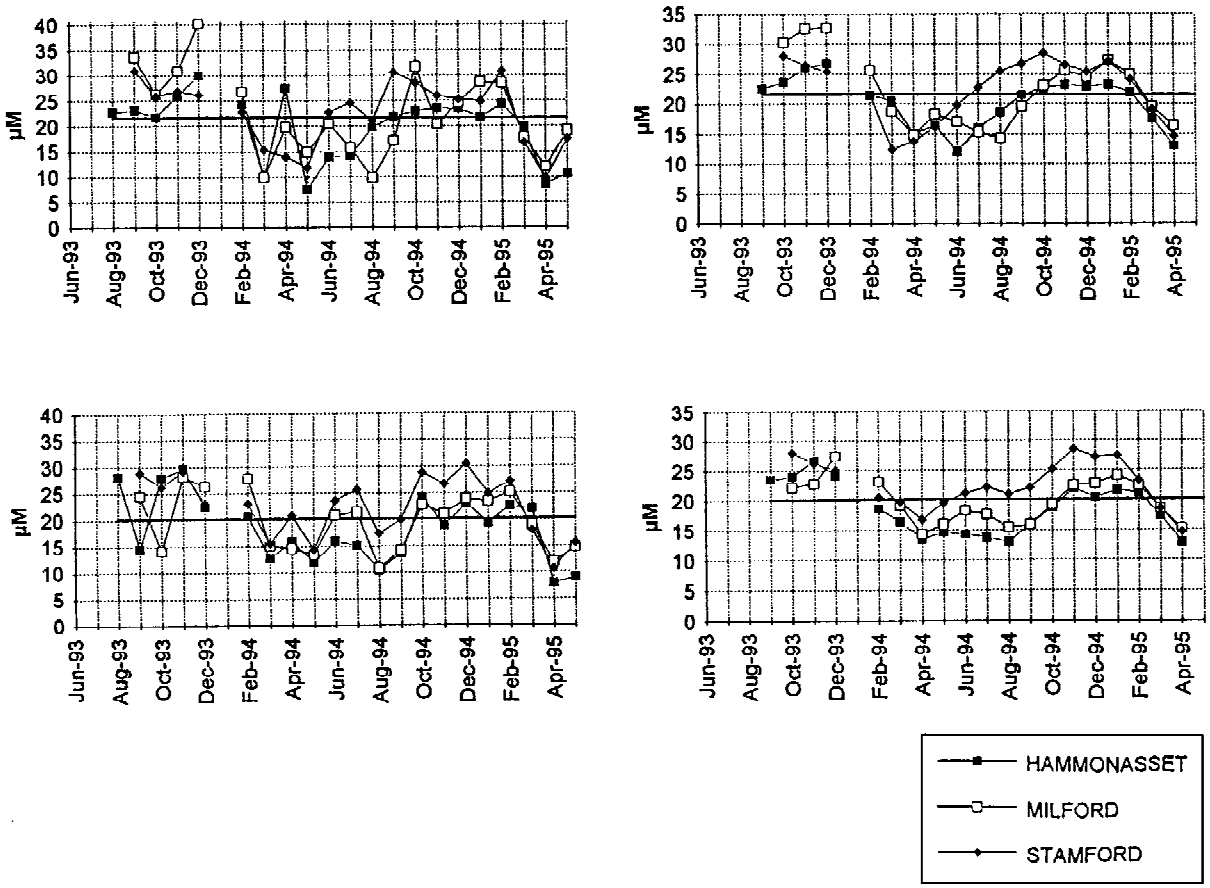


Figure 13. Total dissolved nitrogen (TDN) concentrations in surface (above) and bottom (below) waters, of the 3 study sites. See Figure 10 for data presentation details.

such as LIS (Harris, 1959). In the midst of the seasonal changes, there emerged trends of east–west increase in TN, TDN, DON, PON, DIN, NO_x, and NH_3 for the period of study as a whole. Although they were small (10–20%), these trends may be meaningful because they cover 2 years, appeared in every category, and are consistent with an increase in eutrophication from east to west in LIS.

Inorganic phosphorous concentrations

Dissolved ortho-phosphate concentrations follow a well defined seasonal cycle of highs in the fall/winter and lows in the spring/summer. Levels were consistently higher in Stamford surface & bottom waters as compared with Hammonasset waters (Fig. 19 and Table 3). Differences were more pronounced in the bottom waters where concentrations tended to be higher overall, relative to surface waters. Milford concentrations were very similar to Stamford water levels throughout this study.

Dissolved inorganic N & total dissolved N to phosphorous ratios

The Redfield Ratio of 106:16:1 (C:N:P) is the starting point for discussing nutrient ratios important to planktonic organisms. This ratio represents an approximate ideal elemental ratio for phytoplankton and zooplankton. When N:P ratios drop below approximately 16:1, hindrances to balanced growth occur. In reality, the ideal ratio varies much by species. For this reason as deviations from ideal occur differential successes among species result. Nonetheless, on average, for phytoplankton significant decreases in this ratio favor microalgal forms that can supplement their diets heterotrophically (e.g. the dinoflagellates). Typically the Redfield Ratio is calculated based on dissolved inorganic nutrient levels. However, dissolved organic

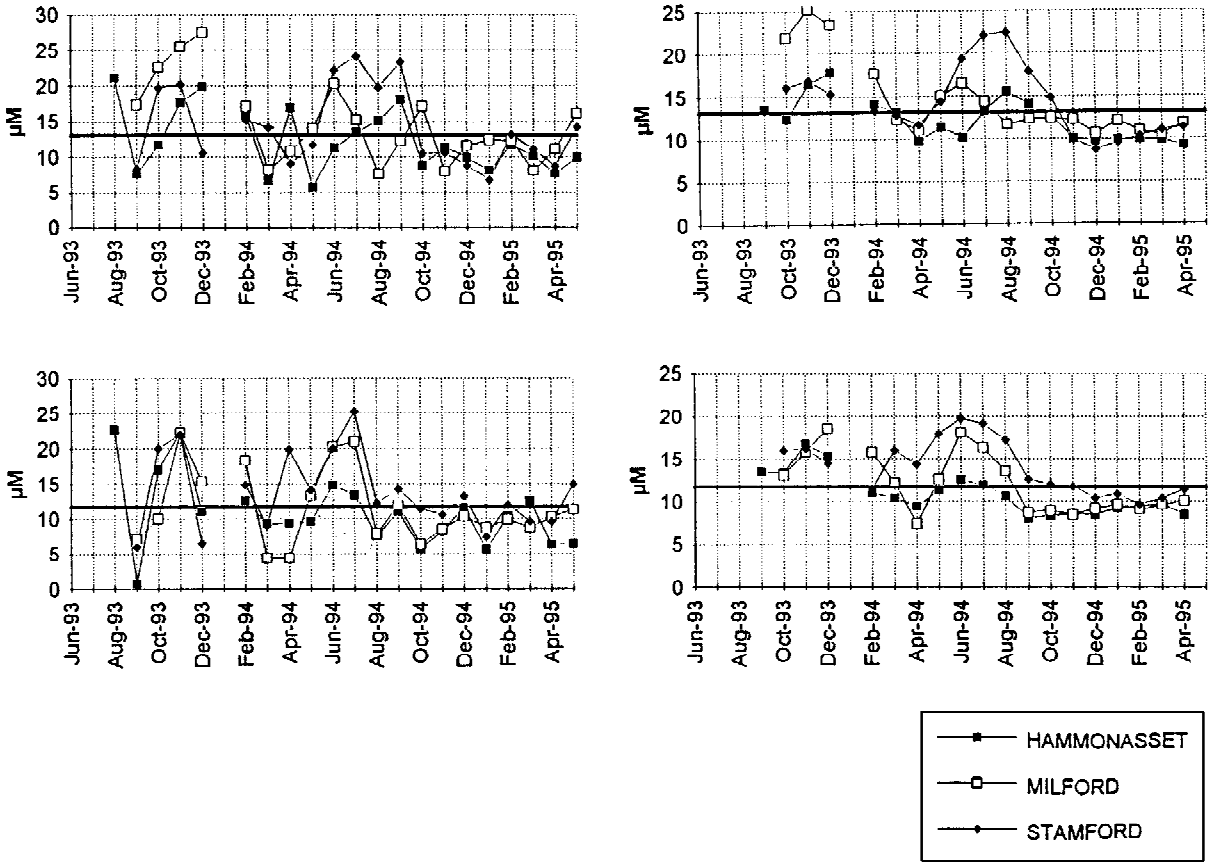


Figure 14. Dissolved organic nitrogen (DON) concentrations in surface (above) and bottom (below) waters, of the 3 study sites. See Figure 10 for data presentation details.

nitrogen (DON) is utilized as a nitrogen source by many (but not all) phytoplanktonic species. It is, therefore, important to calculate N:P ratios based on both inorganic and organic dissolved N levels, as we have done in this study (Tables 5 and 6). Ratios varied much over the year for Long Island Sound nearshore waters. Based on inorganic nutrients only, Stamford waters often exhibited water column values below 10, with an average of 5.6 and 5.8 for years 1 and 2 of this study. Corresponding values of 8.7 and 5.5 for Milford waters and 7.6 and 7.3 for Hammonasset waters were found. Respective bottom water values of 5.1, 7.1 and 6.3 (year 1) and 5.7, 5.4 and 7.2 (year 2) were found for Stamford, Milford and Hammonasset. When total dissolved nitrogen levels are considered, Stamford surface values of 32 and 21.8, Milford levels of 38.1 and 21.3 and Hammonasset levels of 21.8 and 24.5 were found, with respective bottom water values of 27.2 and 17.5 (Stamford), 24.6 and 16.1 (Milford) and 18.8 and 18.8 (Hammonasset) during this study.

Biologically active silica

Dissolved, biologically-available silica was measured because it is a required macro-nutrient for one group of phytoplankton, the diatoms, for incorporation into cell walls. The main sources of BSi in coastal seawater are runoff from shore (Si derived from Chemical weathering of crustal rock), and dissolution of silica minerals (chiefly old diatom shells) in bottom sediments. Dissolution rates of diatom shells are slow, so that little recycling occurs in the water column. Removal of BSi from solution can be attributed almost entirely to uptake by diatoms. Hence, the BSi content of a parcel of water represents the potential for that water to support diatom growth, assuming that all other algal nutrients are present as well.

The theory that nitrogen (N) limits phytoplankton production in Long Island Sound (LIS) is not inconsistent with the hypothesis that BSi limits diatom production. Indeed, human activities have been

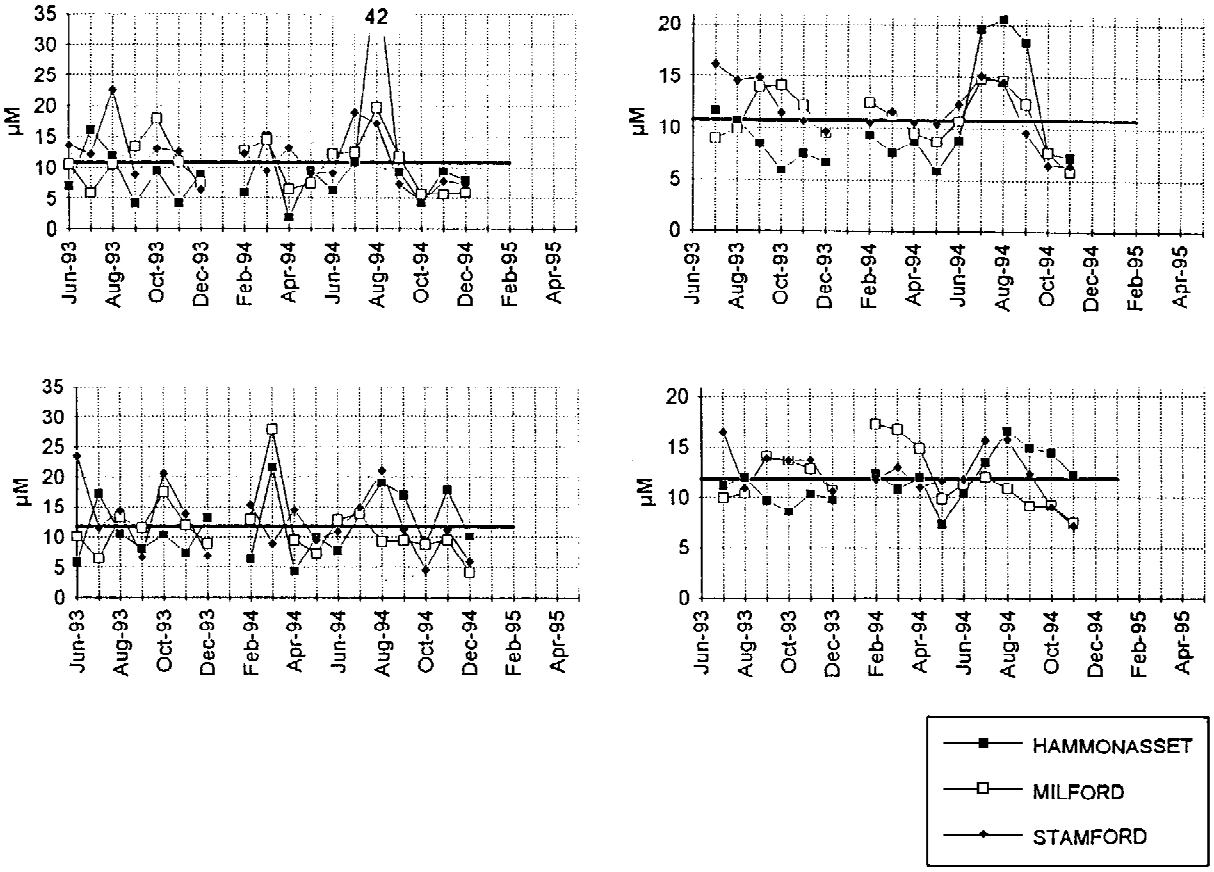


Figure 15. Particulate nitrogen (PN) concentrations in surface (above) and bottom (below) waters, of the 3 study sites. See Figure 10 for data presentation details.

shown to increase N inputs; whereas, we have done relatively little to increase BSi inputs into LIS. Hence, N over-enrichment has two potential effects upon phytoplankton production in LIS: (1) to increase total phytoplankton production, and (2) to increase the percentage of phytoplankton production attributable to non-diatom algal taxa. Whether primary production is in the form of diatoms or other algal cells can have consequences to higher trophic levels if diatoms are better (or worse) sources of food for certain herbivores. One algal taxonomic group that may grow in the absence of diatoms – the dinoflagellates – has the potential to disrupt pelagic food webs through production of toxic metabolites. Biologically available silica, therefore, plays a pivotal role in ecological consequences of N over-enrichment.

BSi concentrations in LIS seawater during this study ranged from <1 μM to approximately 60 μM (Figs 20–22), with one exceptionally high value of 180 μM in Stamford bottom waters in July of 1993. We attribute this high BSi value to enhanced dissolution of sediment Si during an hypoxic event, but cannot confirm this since we did not measure dissolved oxygen in 1993. The most noticeable variation in BSi occurred seasonally. During most of the summer of 1994, BSi values remained in the range of 5–10 μM. As a general rule of thumb, BSi concentrations between 5 and 2 μM become limiting to diatoms (Egge & Aksnes, 1992). Thus, it appears likely that diatoms may have been limited by BSi during the summer of 1994. The increase in BSi during autumn and winter is an expected consequence of light-limited diatom growth. Why BSi concentrations remained low during the winter of 1993–94 is somewhat puzzling, but this observation does demonstrate the range of inter-annual variability.

Although seasonal changes in BSi are clear, differences between sites are less obvious from a simple plot. Mean BSi values for the three sites, averaged for both surface and bottom waters for the entire study period, reveal slightly higher BSi in Stamford

Table 3. Summary of total nitrate, ammonia, inorganic nitrogen, and reactive phosphate concentrations for the 3 stations over the entire study period. Ammonia and phosphate values are presented as total water column averages, as well as separately for surface and bottom waters. All other values represent total water column averages

Average total nitrate (μg-at-N/L)				
	92–93	93–94	94–95	
Stamford	7.7	5.7	7.3	
Milford	8.3	4.7	6.6	
Hammonasset		4.8	5.8	
Average total ammonia (μg-at-N/L)				
	Stamford	*Milford*	*Hammonasset*	
1992–1993				
Surf.	1.5	1.3		
Bot.	2.3	2.3		
Water column	1.9	1.8		
1993–1994				
Surf.	1.3	0.90	1.4	
Bot.	2.9	1.3	1.8	
Water column	2.1	1.1	1.6	
1994–1995				
Surf.	1.2	1.0	1.2	
Bot.	1.4	1.0	1.5	
Water column	1.3	1.0	1.4	
Average total inorganic nitrogen (μg-at-N/L)				
	92–93	93–94	94–95	
Stamford	10.4	8.8	8.9	
Milford	11.9	6.5	7.9	
Hammonasset		7.1	7.5	
Average reactive phoshate (μg-at-P/L)				
	Stamford	*Milford*	*Hammonasset*	
1993–1994				
Surf.	1.1	1.0	1.0	
Bot.	1.4	1.3	1.1	
Water column	1.3	1.1	1.0	
1994–1995				
Surf.	1.3	1.3	0.92	
Bot.	1.4	1.4		1.0
Water column	1.3	1.3	0.96	

and Milford than in Hammonasset (Figs 20–22), but this difference is not statistically significant (ANOVA $p>0.05$). The difference between surface and bottom waters, summed for the entire study, was statistically significant (ANOVA $p>0.05$), with bottom waters containing more BSi. It is interesting to note that the difference between surface and bottom BSi in Stamford is more pronounced than is the case for Milford and Hammonasset. In fact, BSi is slightly lower in Stamford surface waters than in Milford or Hammonasset surface waters; this difference suggests that diatoms in Stamford surface waters are at least as likely to be Si-limited as diatoms in surface waters of Milford and Hammonasset. Furthermore, a larger

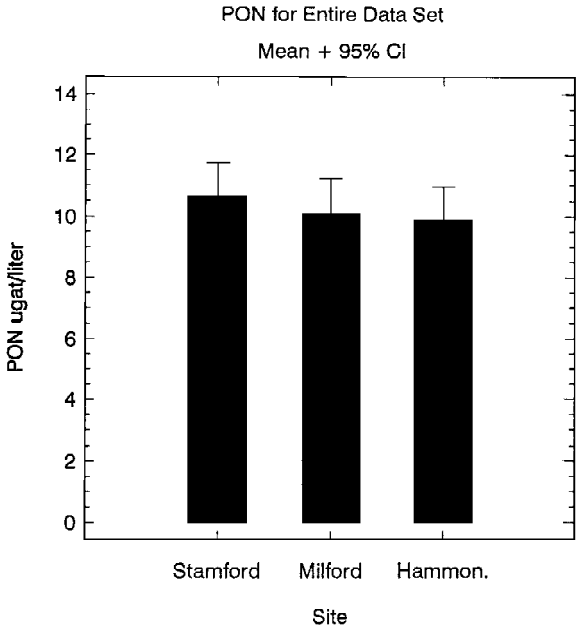


Figure 16. Water Coumn particulate organic nitrogen (PON) averages (μg-atm l^{-1}), over that part of the study when all 3 stations were measured.

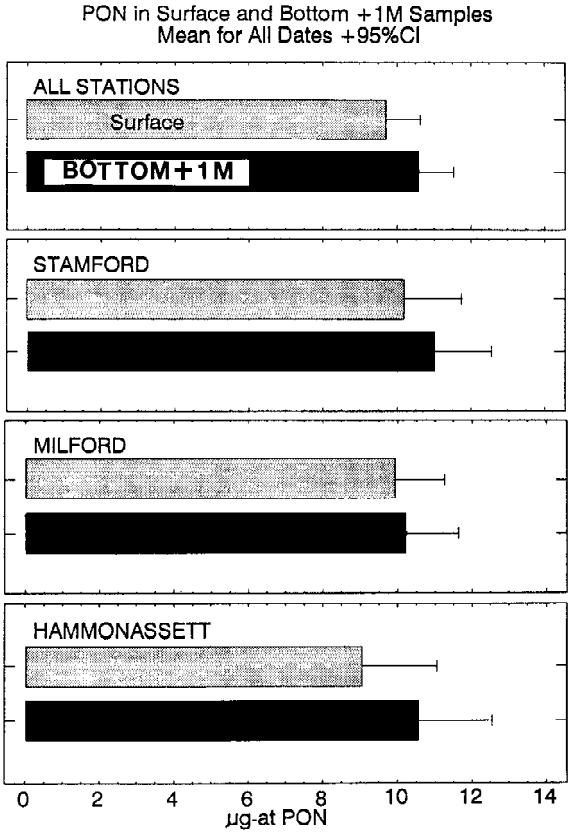


Figure 17. Surface and bottom water pariculate organic nitrogen (PON) concentrations (μg-atm l^{-1}) for the 3 sites, over the period when all 3 stations were sampled.

reservoir of BSi exists in Stamford bottom waters than at the other sites. Assuming that BSi in bottom waters is mainly the result of remineralization of old diatom shells, there is some evidence for enhanced sedimentation of diatoms in western LIS.

Different diatoms, however, have different BSi requirements, often expressed as minimal Si cell quotas, Q_oSi (van Donk & Kilham, 1990). Obviously, larger diatom cells may require more Si per cell than smaller cells, but optimal ratios of Q_oSi: Q_oN for diatoms have been shown to be independent of cell size and species-specific (Tilman et al., 1992), including diatoms isolated from Long Island Sound (Wikfors et al., in review). Questions of Si:N ratios and the importance of lowering the Si:N ratio, by increasing N but not Si, to geographic differences in seasonal phytoplankton community structure in Long Island Sound, are addressed in Wikfors (in review) and Wikfors et al. (in review).

Total & size-fractionated chlorophyll a

Chlorophyll a data

There are four categories of chlorophyll for which data are given: total chlorophyll *a* (Chl), and size fractions of >20 μm (Chl >20), 10–20 μm (Chl 10–20), and <10 μm (Chl <10). All of the more prominent features of strong seasonal cycles of flowering and decline were concurrent among stations (east–west) and between depths (surface–bottom) (Figs 23–26). Minor spatial differences in the cycles did occur, such as comparatively shorter flowerings at Hammonasset, and lack of east–west synchrony of the intermediate chlorophyll fraction (Chl 10–20). Surface and bottom concentrations were well correlated in all categories (<0.01 level of significance), but most strongly in the case of Chl >20. Occurrences of higher chlorophyll in bottom waters (March 1994 for example) could usually be accounted for by Chl >20 (Figs 23–26; Table 8). Occurrences of higher chlorophyll in surface waters (August 1994 at Hammonasset for example) could usually be accounted for by Chl 10–20 and (or) Chl <10 (Figs 23–26 and Table 8). Station-to-station differences in chlorophyll concentrations were clearest when concentrations were high, and less distinct when concentrations were low.

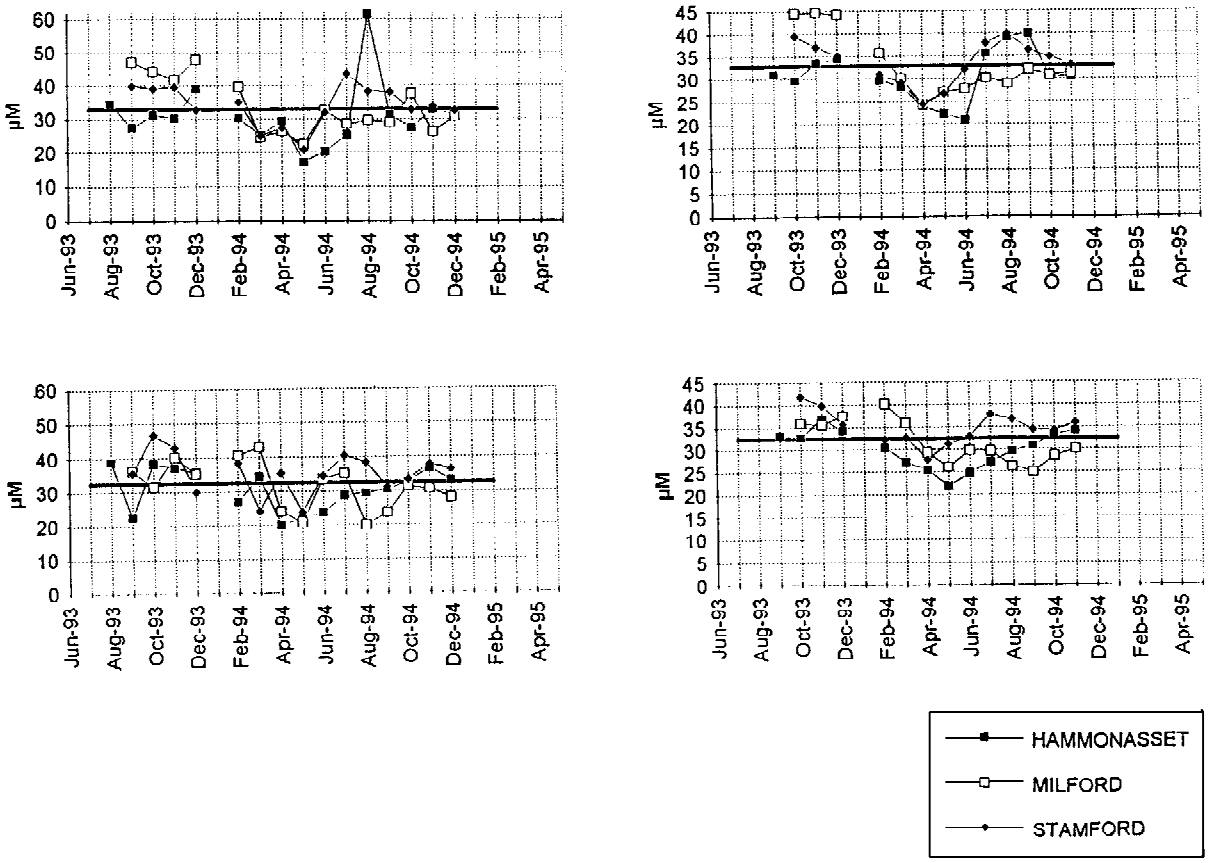


Figure 18. Total nitogen (TN) Concentrations in surface (above) and bottom (below) waters for the 3 study sites. See Figure 10 for data presentation details.

Chlorophyll a

Concentrations ranged between 0.4 and 67 μg l^{-1} at our three stations (Fig. 23). There were peaks in August 1992, April 1993, October 1993, March 1994, August 1994, and April 1995. Peaks in March and April indicate spring blooms, August peaks indicate late summer blooms, and the October peak may be considered a delayed summer, or fall bloom. The August 1992 and April 1993 peaks were lower than the peaks that followed. Spring blooms were less distinct at Hammonasset than at the western stations, as was the October 1993 peak. Hammonasset had the highest concentration in the summer bloom of August 1994. No one station had consistently lowest Chl, but station-to-station differences were consistent enough to produce trends in mean concentration for the period of study (Table 9). There was an increase in the depth average of about 37% between Hammonasset and Milford, and a further increase of about 10% between Milford and Stamford.

Chlorophyll >20µm

Concentrations ranged from 0.2 to 60 μg l^{-1} (Fig. 24). The bulk of the chlorophyll was composed of Chl >20 during winter–spring and fall flowerings, and Chl >20 comprised about 57% of Chl on average at Hammonasset, and about 70% at each of the stations further west, producing the general similarity seen among stations in Figure 23. Seasonal peaks occurred in September 1992, April 1993, October 1993, March–April 1994, October 1994, and March–April 1995. Hammonasset was lowest in the October 1993 peak, the April 1994 peak, the August 1994 peak, and in March but not April of 1995. However, station-to-station differences were consistent enough to produce considerable trends in mean concentration over the period of study (Table 9). There was an overall increase in the depth average of about 61% from Hammonasset to Milford, and an additional small increase of about 5% from Milford to Stamford.

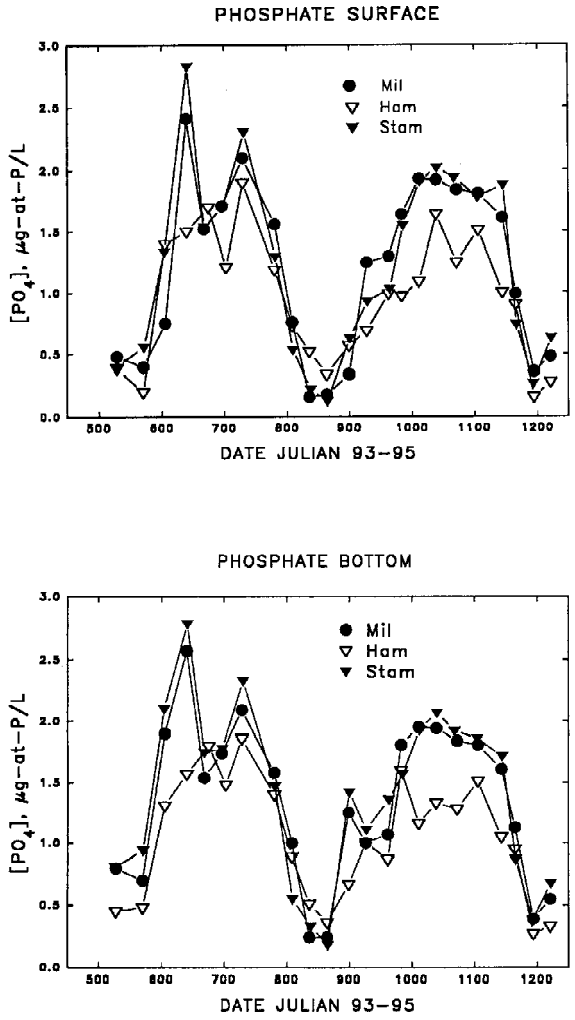


Figure 19. Reactive phosphate concentrations in surface and bottom waters of the 3 study sites.

Chlorophyll 10–20 μm

Concentrations ranged from undetectable to 20 μg l^{-1} (Fig. 26), but only once exceeded 10 μg l^{-1} (August 1994 at Hammonasset). Peaks occurred in August in 1992, 1993, and 1994, and below average values typically occurred from November until March. Although Chl 10–20 comprised on average less than 25% of Chl at Hammonasset, and less than 15% at Milford and Stamford, it made up about half of Chl during the August blooms. No one station had consistently lowest Chl 10-20, however, station-to-station differences were consistent enough to produce trends in mean concentration over the period of study (Table 9). On average, Milford, the center station, had less than Hammonasset, while Stamford was similar to Hammonasset at the surface, and less at the bottom. This reversal of the east–west pattern noted for Chl and Chl >20 is eliminated if the extraordinary peak in Chl 10–20 at Hammonasset in August 1994 is ignored.

Chlorophyll <10 μm

Values ranged from <0.1 to 15 μg l^{-1}, but seldom exceeded 4 μg l^{-1} (Fig. 25). Peaks in Chl <10 occurred around July and August in 1992 and 1994, but not in 1993. This fraction was only about 15 – 20% of Chl on average (Table 8) however, it was as much as 50-75% of Chl in the low months of June and July. The flowering of August 1994 was about 33% Chl <10, the highest percentage observed in any bloom. No one station had consistently lowest Chl <10, however, station-to-station differences were consistent enough to produce overall trends in mean concentration over the period of the study (Table 9). A steady east–west increase occurred at the surface and the bottom.

Chlorophyll summary

Strong seasonal cycles of flowering and decline in chlorophyll stocks occurred concurrently at each station in a manner consistent with the patterns of chlorophyll in temperate estuaries (Riley, 1955). Dominance went to Chl >20 in winter, spring, and fall, and shifted towards the smaller size fractions only in summer. Furthermore, Chl >20 was more abundant on average than the two smaller fractions combined, and it almost entirely dominated all but the August flowerings. There were east–west increases in Chl, Chl >20, and Chl <10 despite more copepod grazers in the west; however, Chl 10–20 did not conform to this pattern. The most conspicuous pattern among stations was the increase between Hammonasset and Milford in the Chl >20 size fraction which dominated Chl, the most positive indication of a eutrophication gradient from east to west in LIS.

Phytoplankton densities

Phytoplankton cell numbers ranged from less than 1 to over 13 million cells per liter in the 1994 Stamford and Hammonasset surface samples counted (Figs 27 and 28). Photosynthetic cells in the <2 μm size range generally represented about 1/3 of the total cell number, as estimated from fluorescence observations; inclusion of the smallest photosynthetic cells in plots did not change seasonal patterns appreciably. The most noteworthy difference in phytoplankton cell numbers between the west and east is not in total counts, but rather in seasonal timing of peaks. Algal cell numbers

Table 4. Mean value and average percentage of total nitrogen for seven nitrogen parameters for the period when all 3 stations were sampled (June 1993 – May 1995) as well as their east–west trends. Row labels are grouped according to the way the parameter was measured as follows: Dir=direct measure; Sum=sum of 2 measures; dif=difference between two measures; Bot=bottom and surf=surface

Parameter measured by			Hammonasset		Milford		Stanford		Trends between stations	
Sum	Dir.	Dif.	Mean μM	%TN	Mean μM	%TN	Mean μM	%TN	Ham-Mil	Mil-Stam
	SURF-TDN		19.9	65	22.4	66	22.7	66	+13%	+1%
	BOT-TDN		18.3	63	19.6	64	22.5	64	+7%	+15%
	SURF-PN		10.2	35	10.7	34	11.4	37	+5%	+7%
	BOT-PN		11.6	37	11.4	36	12.5	36	–2%	+10%
SURF-TN			30.9	100	33.8	100	34.1	100	+9%	+1%
BOT-TN			30.9	100	31.6	100	35.3	100	+3%	+12%
	SURF-NOx		5.8	19	5.6	18	6.3	18	–3%	+13%
	BOT-NOx		5.4	18	6.3	20	6.7	19	+17%	+6%
	SURF-NH3		1.3	4	1.3	4	1.3	4	0	0
	BOT-NH3		1.7	6	1.4	4	1.9	5	–18%	+35%
SURF-DIN			7.1	23	6.9	20	7.6	22	–3%	+10%
BOT-DIN			7.0	23	7.1	22	8.6	24	+1%	+21%
		SURF-DON	11.7	38	14.0	41	13.5	40	+20%	–4%
		BOT-DON	10.4	35	11.4	36	13.2	37	+10%	+16%

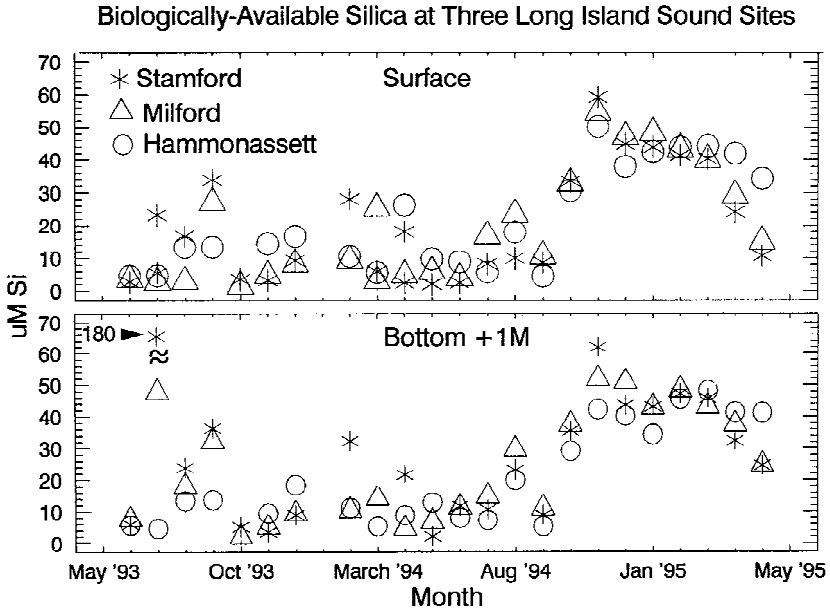


Figure 20. Biologically available Silica (BSi) concentrations in surface and bottom waters of the 3 study sites. Units = μmoles of Silica.

increased in July and August in Hammonasset, and in October in Stamford (Figs 27 and 28).

Considering only the >2 μm phytoplankton, that could be counted in fixed samples, differences in timing of shifts from diatom to non-diatom taxa accompanied seasonal changes in total counts. In Stamford, dinoflagellates replaced diatoms almost entirely in July; at this time, cryptophycean algae bloomed to high numbers in Hammonasset. The accumulation of phytoplankton cells observed in Hammonasset during August and September were mainly dinoflagellates. Differences in peak timing and taxonomic composi-

Table 5. Dissolved inorganic nitrogen to phosphate ratios, and total dissolved nitrogen (TDN) to phosphate ratios for surface and bottom water samples from the 3 stations

	Stamford		Milford		Hammonasset	
Date	Surf	Bot	Surf	Bot	Surf	Bot
N/P Ratios						
6/93	3.3	7.3	4.2	7.1	7.6	9.3
7/93	0.3	5.5	0.8	0.8	9.8	1.3
8/93	1.5	6.6	2.8	2.5	1.3	4.2
9/93	9.5	8.2	6.8	6.8	10	8.7
10/93	4.1	3.6	2.4	2.6	6.0	6.1
11/93	4.0	4.1	3.2	3.4	6.8	5.0
12/93	6.8	7.1	6.1	5.3	5.4	6.1
2/94	5.9	5.6	5.7	6.0	7.2	5.7
3/94	2.4	4.1	2.2	1.3	4.3	3.8
4/94	22.3	2.7	55.8	42.2	20.5	12.8
5/94	1.3	1.0	5.3	0.7	5.3	6.5
93–94 Average	5.6	5.1	8.7	7.1	7.6	6.3
6/94	0.8	2.6	0.8	0.5	4.8	1.7
7/94	0.4	2.6	0.5	0.5	1.3	1.8
8/94	1.3	3.8	1.7	2.7	4.6	3.3
9/94	4.7	3.7	3.1	2.8	3.9	1.6
10/94	9.4	9.0	7.6	7.2	13.1	15.9
11/94	7.6	7.8	6.5	6.5	8.0	7.9
12/94	8.5	8.9	7.2	7.4	10.9	8.9
1/95	10.2	9.4	9.0	8.2	9.1	9.3
2/95	9.5	9.0	10.1	9.4	12.7	11.6
3/95	7.8	9.6	9.9	9.1	10.8	11.0
4/95	3.9	2.8	2.8	4.4	5.5	5.5
5/95	5.3	1.0	6.4	6.2	2.5	7.5
94–95 Average	5.8	5.7	5.5	5.4	7.3	7.2
TDN/P Ratios						
9/93	11.0	10.4	14.0	9.5	15.5	9.2
10/93	16.9	15.0	17.3	9.1	12.8	15.8
11/93	15.9	16.4	18.1	16.2	21.5	20.1
12/93	11.3	9.9	19.1	12.6	15.8	12.0
2/94	17.6	15.7	17.1	17.6	20.4	14.7
3/94	28.7	28.0	13.0	15.1	13.4	14.3
4/94	63.6	63.0	123.0	60.4	52.9	31.2
5/94	91.5	79.4	82.8	56.3	22.4	33.1
93–94 Average	32.1	27.2	38.1	24.6	21.8	18.8
6/94	32.6	16.6	60.0	16.6	24.6	23.7
7/94	26.5	23.1	12.6	21.4	20.7	15.1
8/94	20.5	12.8	7.5	10.0	19.9	12.0
9/94	19.8	12.7	10.5	7.8	22.6	8.5
10/94	14.9	14.9	16.4	11.6	21.1	20.8
11/94	12.9	12.9	10.6	10.9	14.3	14.1
12/94	13.0	15.8	13.4	12.9	18.7	17.9
1/95	14.0	13.4	15.9	12.9	14.4	12.8
2/95	16.5	15.8	17.7	15.6	24.3	21.4
3/95	22.7	20.7	17.8	16.7	22.0	23.1
4/95	36.3	27.9	33.5	30.5	53.8	28.9
5/95	28.0	22.9	40.0	26.7	38.0	27.0
94–95 Average	21.8	17.5	21.3	16.1	24.5	18.8

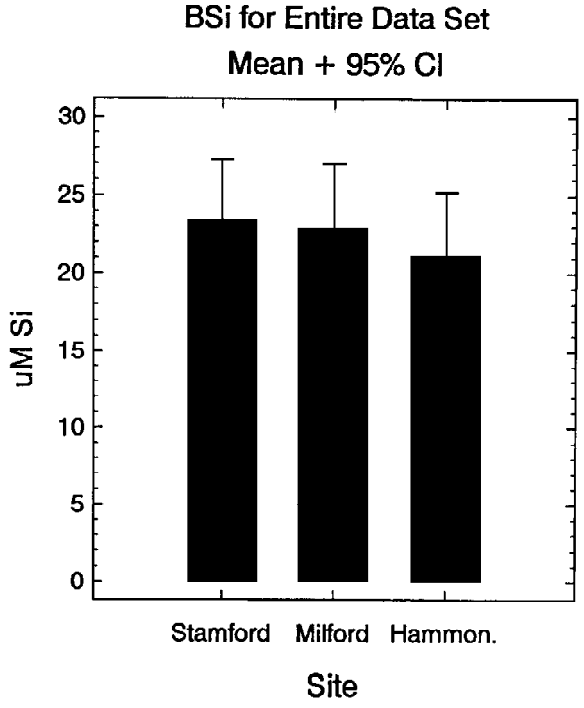


Figure 21. Mean, whole water column, BSi Concentrations averaged over the entire study period for all 3 stations.

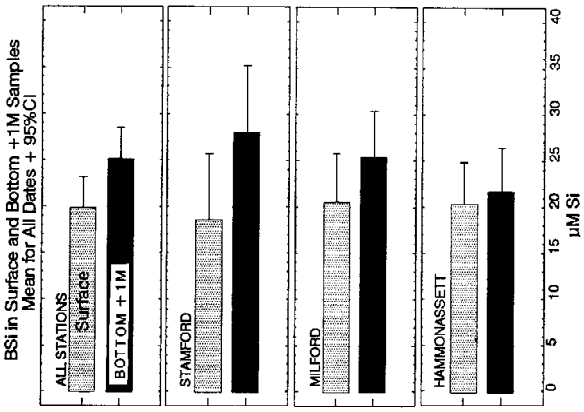


Figure 22. Mean water column biologically available silica concentrations presented separately for surface and bottom water, averaged over the entire study period, for all 3 stations.

tion of phytoplankton assemblages between Stamford and Hammonasset were clear and pronounced, and are likely controlled by both bottom-up (nutrient) and top-down (grazing) factors.

Photosynthetic nanoplankton (PNANS)

Photosynthetic nanoplankton densities varied from a low of 0.2×10^4 to a high of 7.5×10^4 per ml. (Fig. 29), with well developed seasonal peaks in summer.

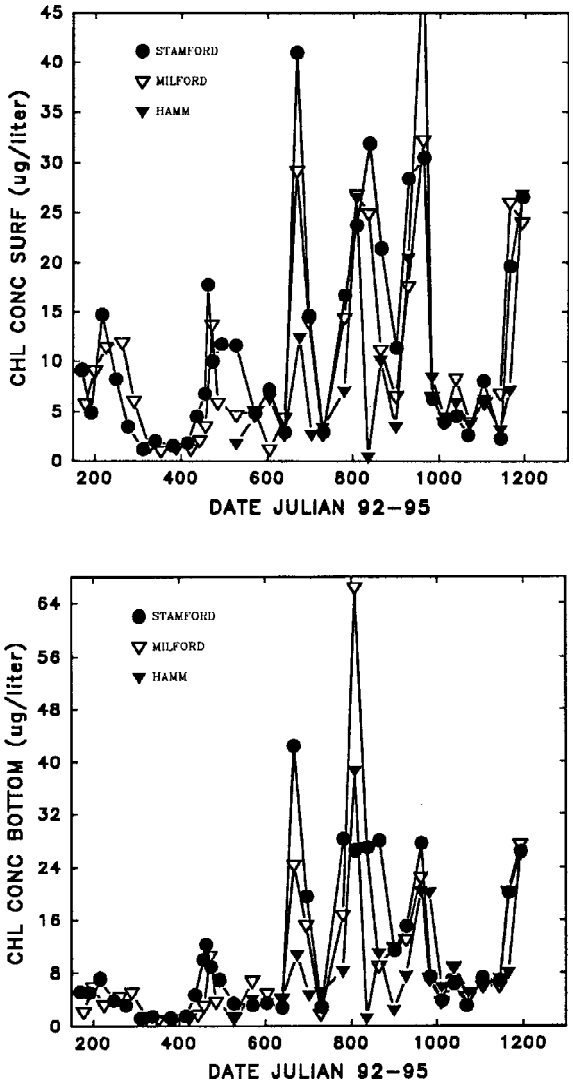


Figure 23. Total surface and bottom water chlorophyll *a* concentrations (as $\mu g\, l^{-1}$) over the entire study, for the 3 stations.

Densities were higher in surface waters where light is more available. Surface and bottom water seasonal trends were identical as were spatial trends among our 3 sampling sites. Differences among stations were slight but for key summer peaks where the Hammonasset site exhibited concentrations 1.5 – 3 times higher than the more western sites.

Bacterial densities & frequency of dividing cells

Bacterial densities varied from winter lows of about 0.3×10^6 per ml to typical summer highs of $3 – 5 \times 10^6$ per ml in both surface and bottom waters at all 3 of our stations (Fig. 30). Of great interest was the dis-

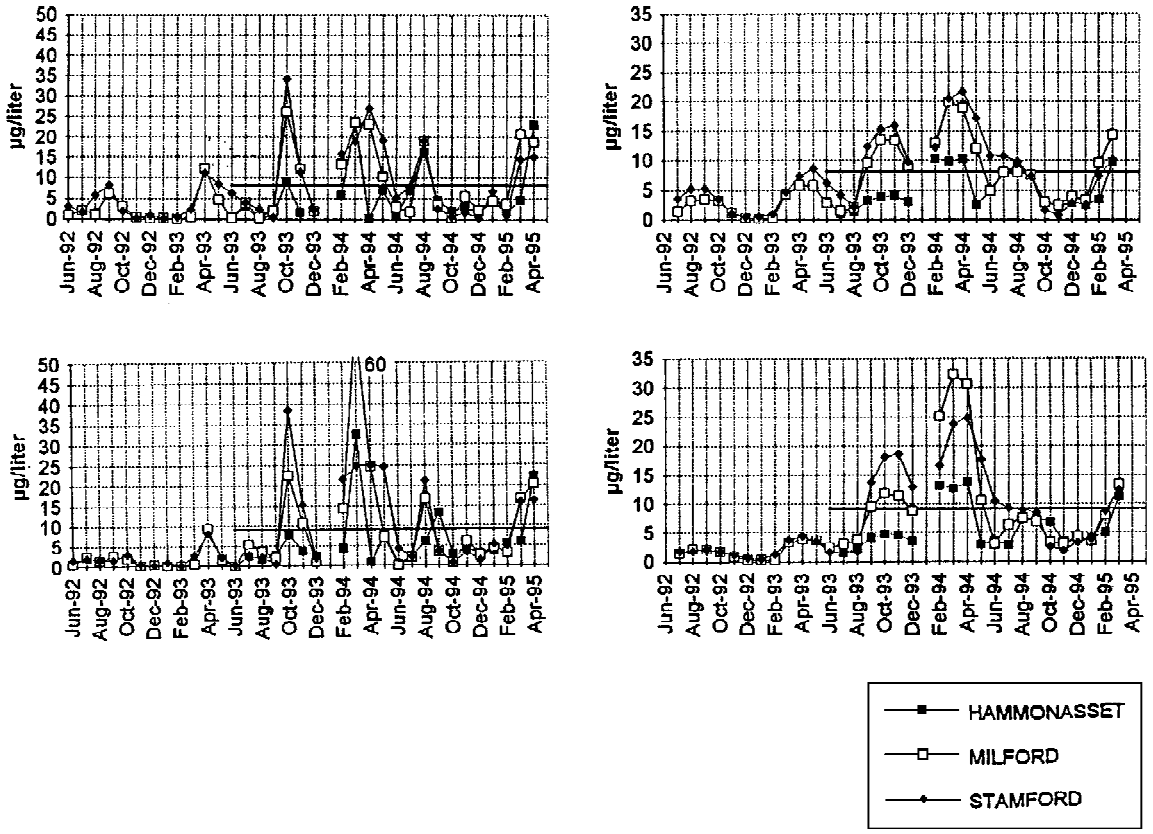


Figure 24. Greater than 20 μm chlorophyll *a* concentrations in surface (above) and bottom (below) waters. See Figure 10 for details on data presentation.

covery of a clear, multi year, repetative seasonal cycle of high *versus* low densities in the surface and bottom waters of all 3 stations. It has been generally assumed until now that no patterns of bacterial abundance exist in coastal marine/estuarine waters. Gradients in abundance do exist from west to east with our western station waters generally exhibiting slightly higher bacterial densities than our eastern station waters, in the summer. No such differences are found between our central and western station waters. One extremely high summer value of 9×10^6 per ml (3 times higher than the other 2 stations) was observed at our western station. This high corresponded to an extreme high silicate value (Fig. 20) and we believe it to be an hypoxic-related effect.

Frequency of dividing cells data, which represent an approximate measure of bacterial growth rates, were similar in surface and bottom waters, and varied between 2% and 7.5% with summer values, in particular, higher in western station waters as compared to eastern station waters (Fig. 31).

Heterotrophic nanoplankton densities

Heterotophic nanoplankton densities were similar in surface and bottom waters of all 3 stations and stations were similar to each other in terms of seasonal patterns. Overall densities on average varied between 0.1×10^3 and 6.4×10^3 per ml, with significant east to west variations at times, and with the central to western station waters sporting higher concentrations than eastern station waters (Fig. 32). Of most note was the extreme interannual differences that appeared between the 1992–93 and 1993–94 sampling seasons.

Phytoplankton species composition & semi-quantitative population estimates

Lists of phytoplankton taxa identified at the three LIS sites during 1993-1995, are presented in Table 10. Total numbers of species found were not remarkably different for different sites; however, identities of dominant taxa varied considerably from site to site. For 1993, during which we sampled Hammonasset

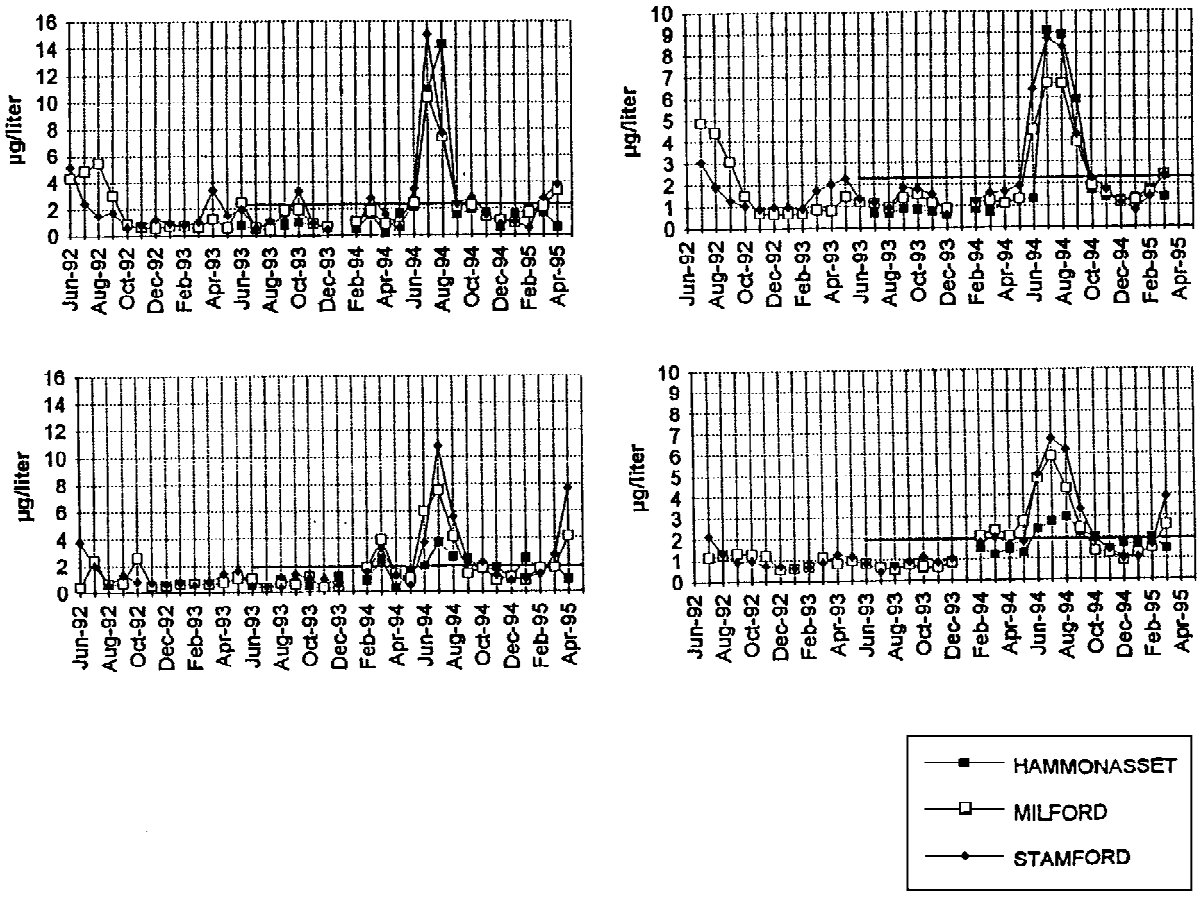


Figure 25. Less than 10 μm chlorophyll *a* concentrations in surface (above) and bottom waters. See Figure 10 for details on data presentation.

for only half the year, eight of 15 dominant phytoplankton taxa in Stamford were not included in the listing of dominants for Hammonasset. Conversely, 7 of 15 Hammonasset dominant taxa were not listed as dominants in Stamford (Table 10). For 1994, the only year with a full sampling schedule, five of 14 Stamford dominants were not even recorded at Hammonasset, whereas, six of 20 Hammonasset dominants were not found in Stamford (Table 10). Finally, in 1995, for which we sampled only winter and spring, nine of 15 Stamford dominants were not dominants in Hammonasset, and two of eight Hammonasset dominants were not dominant in Stamford (Table 10). From this simple listing, it is clear that phytoplankton community structure is different at the three sites.

Percentages of phytoplankton assemblages accounted for by major taxonomic groups also revealed seasonal differences between sites (Fig. 33). For all three sites, centric diatoms tend to dominate the winter and early spring flora, but pennate diatoms occasionally contribute considerably, especially in bottom waters where benthic taxa may be mixed into the water column. Dinoflagellates showed a major pulse in Stamford and Milford during the summer of 1992, with more modest increases in 1993–1994. Hammonasset experienced a significant increase in dinoflagellates during the summer of 1994, and overall had study-averaged lower concentrations of dinoflagellates than either the central or western stations (Fig. 33). Green algae and crytophytes remained only minor floral constituents, with one or two exceptions.

Occasionally, e.g. spring of 1993 at Stamford and Milford and August of 1994 in Hammonasset, picoplanktonic cells (<2 μm) showed strong dominance; it is impossible to identify these cells with light or fluorescent microscopy. In most cases, bottom and surface waters tracked each other fairly well, resulting from lack of stratification and deposition of surface algae to bottom waters. An exception to this is that dinoflagellates tended to be slightly more abundant in

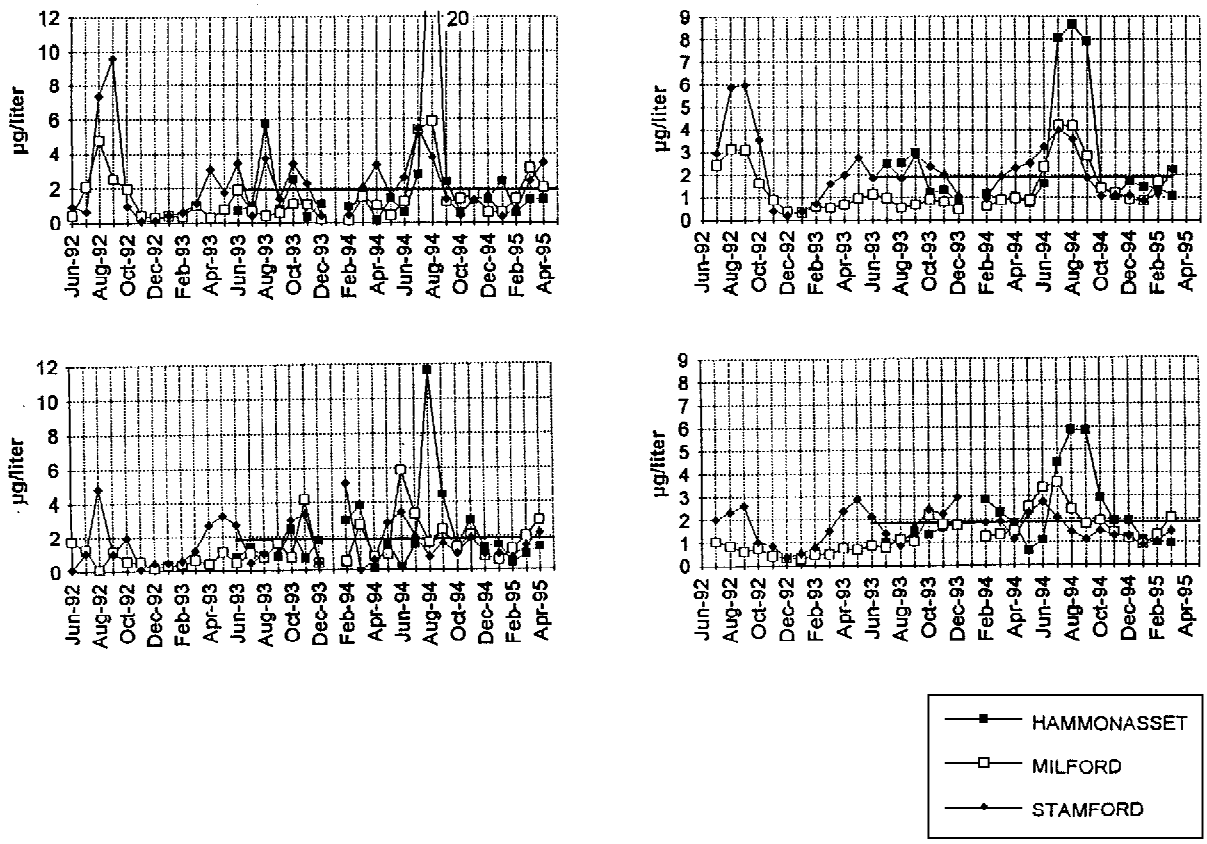


Figure 26. Ten –20 μm chlorophyll *a* concentrations in surface (above) and bottom (below) waters. See Figure 10 for details on data presentation.

surface waters than in bottom, resulting possibly from depth regulation by the dinoflagellates themselves or lower sinking rates because of less grazing. Seasonal shifts in major phytoplankton groups generally followed expected patterns, but differences in identities of dominant taxa and timing of shifts were apparent for the different sites.

Water column ciliate species composition

Prior to this study about 28 species of water column ciliates (mostly tintinnids) have been reported for the waters of Long Island Sound (Capriulo & Carpenter, 1983). This study extends the list of species to 71 (Table 11). Differences in species composition among stations were found on most of the sampling dates. A summary of the 1993–94 and the 1994–95 sampling periods indicates that of the 71 species encountered 94% of them were observed in our western station waters, while 80% occurred in our central station waters and only 62% in the waters of our eastern most station (Table 12). Additionally, some differences were encountered between surface and bottom waters of the same station for all 3 stations. Seasonal data on when various species of ciliates were present in the Sound at each of the respective sites will be presented in a future contribution (Capriulo & Pellet, in prep.).

Copepod abundance & species composition

Standing stocks varied between 183 and 64 152 individuals per cubic meter (Table 13). There were pronounced annual cycles in copepod abundance (Fig. 34). Stocks were generally high from mid-spring through early-summer, and generally low from mid-summer through winter. The amplitude of the seasonal cycle increased west of Hammonasset, and the range at the western station was about five times that of Hammonasset. The arithmetic and geometric means (Table 13 and Fig. 34) suggested a sharp increase in copepods between Hammonasset and Milford, but not much difference between Milford and Stamford.

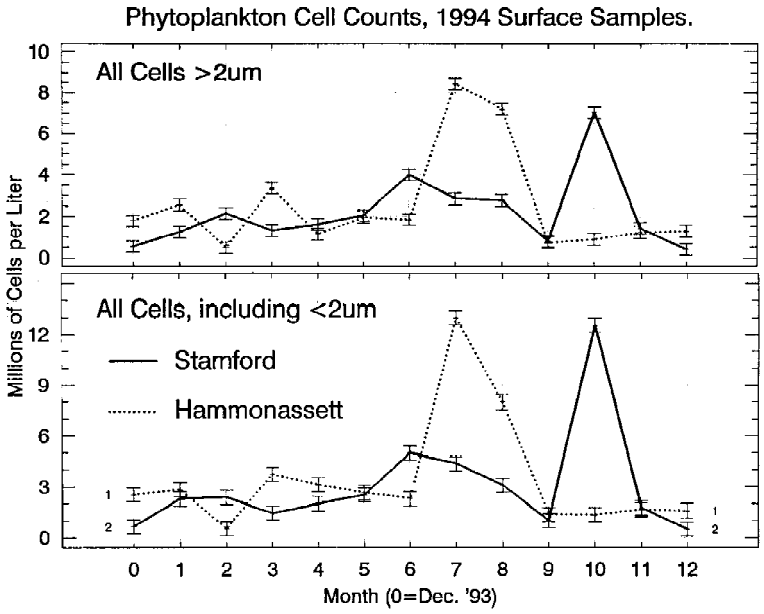


Figure 27. Quantitative phytoplankton cell counts for 1994 surface samples from the Stamford and Hammonasset stations, for all cells greater than 2 μm (top), and all cells including the less than 2 μm (bottom) sizes.

Table 6. Whole water column dissolved inorganic nitrogen to phosphate ratios, and total dissolved nitrogen (TDN) to phosphate ratios, for the 3 study sites

	Stamford	Milford	Hammonasset
Dissolved inorganic nitrogen/phosphate ratio			
1993–1994			
Average	5.4	7.9	7.0
1994-1995			
Average	5.8	5.5	7.3
1993–1995			
Average	5.4	6.3	7.2
Total dissolved nitrogen/phosphate ratio			
1993–1994			
Average	29.7	31.4	21.1
Median	16.7	17.2	17.8
1994-1995			
Average	19.7	18.7	21.7
Median	16.5	15.7	21.1
1993–1995			
Average	24.1	23.8	21.1
Median	16.5	16.3	20.3

Table 7. Correlations between surface water and bottom water concentrations for total chlorophyll as well as each of the 3 size fractions of chlorophyll examined in this study

Parameter	*r*	*p*
Chl	0.80	<0.01
Chl >20	0.88	<0.01
Chl 10–20	0.63	<0.01
Chl <10	0.75	<0.01

The amount of increase between Hammonasset and Milford appeared to be affected by season, since the difference was most noticeable in the late spring. The highest numbers in all statistical categories (Table 13) occurred at Milford rather than Stamford.

The possibility of net clogging was evaluated during 37 of the 102 tows. The ratio of a flow meter positioned inside the mouth of the net to a meter positioned outside provided rough estimates of the nets filtration efficiency (UNESCO, 1968). Those ratios varied from a minimum of 0.38 to a maximum of 1.06, with a mean of 0.83 and a median of 0.84. It is arguable that filtration efficiencies estimated by inside and outside flowmeters are biased towards lower values. The nets forward motion can displace and accelerate water, causing an increase in the rate of flow through the outside flowmeter as the flow through the inside decreases (UNESCO, 1968). Nevertheless, the

Table 8. Chlorophyll size-fractionation data (for the 3 size-fractions: >20, 10–20, and <20 μm) as percentage of total

Month	Size-Fractionated Chlorophyll Percentages								
	Stamford			Milford			Hammonasset		
	>20 μm	10–20 μm	<10 μm	>20 μm	10–20 μm	<10 μm	>20 μm	10–20 μm	<10 μm
Surface									
6/18/92	34.0	10.0	56.0						
6/26/92				18.0	7.0	75.0			
7/9/92	38	13.0	49.0						
7/17/92				23.0	23.0	54.0			
8/3/92	39.5	5.0	10.5						
8/12/92				10.6	42.0	47.6			
9/4/92									
9/18/92				53.0	22.0	25.0			
10/2/92	55.0	27.0	18.0						
10/16/92				48.0	32.0	14.0			
11/6/92	29.0	8.0	63.0						
11/20/92				29.0	26.0	45.0			
12/4/92	45.0	5.0	60.0						
12/18/92				22.0	25.0	53.0			
1/15/93	14.0	27.0	59.0						
1/23/93				16.0	29.0	55.0			
2/19/93	27.0	31.0	42.0						
2/26/93				11.0	30.0	59.0			
3/12/93	53.0	25.0	22.0						
3/19/93				25.0	46.0	29.0			
3/31/93	72.0	7.0	21.0						
4/2/93				71.0	13.0	16.0			
4/7/93	63.0	18.0	19.0						
4/18/93	35.0	25.0	40.0						
4/30/93				77.0	13.0	10.0			
5/8/93	72.0	15.0	13.0						
6/10/93	54.0	30.0	17.0						
6/11/93				7.0	40.0	53.0	18.0	38.0	43.0
7/23/93				76.0	13.0	11.0	67.0	22.0	11.0
7/24/93	81.0	8.0	11.0						
8/26/93	34.0	51.0	15.0						
8/27/93				36.0	32.0	32.0	0	86.0	14.0
10/1/93				45.0	13.0	43.0	45.0	28.0	27.0
10/2/93	13.0	48.0	39.0						
10/29/93	84.0	8.0	8.0	90.0	4.0	7.0			
11/5/93							72.0	20.0	8.0
11/26/93				86.0	7.0	6.0			
11/27/93	78.0	16.0	6.0						
12/3/93							61.0	12.0	27.0
12/29/93				70.0	7.0	23.0	52.0	32.0	16.0
12/31/93	72.0	13.0	15.0						
2/18/94				92.0	1.0	7.0	80.0	13.0	7.0
2/19/94	95.0	3.0	3.0						
3/18/94				88.0	5.0	7.0	88.0	6.0	6.0
3/19/94	80.0	8.0	12.0						

Continued on p. 303

Table 8. contd.

Month	Size-Fractionated Chlorophyll Percentages								
	Stamford			Milford			Hammonasset		
	>20 μm	10–20 μm	<10 μm	>20 μm	10–20 μm	<10 μm	>20 μm	10–20 μm	<10 μm
4/15/94				92.5	4.1	3.4	41.6	30.5	27.8
4/17/94	88.0	7.0	5.0						
5/13/94				91.0	3.6	5.5	69.5	14.2	16.3
5/14/94	90.2	7.3	2.7						
6/17/94				43.4	24.1	32.5	22.1	15.2	62.6
6/18/94	45.6	23.3	31.1						
7/15/94				10.3	30.7	59.0	30.3	14.1	55.6
7/16/94	28.0	19.2	52.8						
8/19/94				61.5	14.8	23.7	31.5	54.5	13.9
8/21/94	62.3	12.5	25.2						
9/9/94				49.3	17.9	32.8	53.6	28.3	18.1
9/11/94	40.5	22.3	37.2						
10/7/94				6.9	35.5	57.6	45.5	11.9	42.6
10/8/94	17.3	10.8	71.9						
11/4/94				64.6	18.6	16.8	47.5	24.2	28.3
11/5/94	36.1	29.5	34.4						
12/3/94	28.2	39.2	32.6						
12/7/94				56.1	15.2	28.8	48.8	36.0	15.2
1/9/95	83.6	4.1	12.3						
1/10/95				74.6	9.9	15.5	68.3	12.9	18.8
2/17/95				55.6	20.1	24.3	55.6	21.5	22.9
2/18/95	45.5	32.7	21.9						
3/10/95				79.5	12.1	8.3	62.9	22.0	15.1
3/11/95	73.4	12.3	14.3						
4/7/95				77.9	8.0	14.0	85.4	7.0	7.6
4/8/95	56.6	13.0	30.4						
5/5/95				10.8	42.6	46.7	64.8	16.3	18.9
5/6/95	21.4	6.8	71.8						
Bottom									
6/18/92	30.0	1.9	71.9						
7/9/92	40.0	21.0	39.0						
7/17/92				39.0	21.0	40.0			
8/3/92	23.0	68.0	9.0						
9/4/92	40.0	26.0	34.0						
9/18/92				59.0	25.5	15.5			
10/2/92	39.9	8.4	52.0						
10/16/92				39.0	11.0	50.0			
11/6/92	17.4	31.0	51.4						
11/20/92				24.0	39.6	36.7			
12/4/92	9.0	41.0	50.0						
12/18/92				37.5	13.5	49.0			
1/15/93	50.0	25.0	16.0						
1/23/93				16.0	30.0	54.0			
2/19/93	68.0	17.0	15.0						
2/26/93				17.0	30.0	53.0			
3/12/93	67.0	22.0	11.0						
3/19/93				28.0	38.0	34.0			
3/31/93	89.0	4.0	7.0						
4/7/93	61.0	11.0	28.0						
4/16/93				74.0	7.0	19.0			

Continued on p. 304

Table 8. contd.

Month	Size-Fractionated Chlorophyll Percentages								
	Stamford			Milford			Hammonasset		
	>20 μm	10–20 μm	<10 μm	>20 μm	10–20 μm	<10 μm	>20 μm	10–20 μm	<10 μm
4/18/93	31.0	46.0	23.0						
4/30/93				42.0	30.0	28.0			
6/10/93	9.0	77.0	14.0						
6/11/93				0	33.0	67.0	12.0	53.0	35.0
7/23/93				80.0	15.0	5.0	61.0	33.0	6.0
7/24/93	72.0	16.0	13.0						
8/26/93	63.0	27.0	10.0						
8/27/93				73.0	15.0	12.0	49.0	25.0	26.0
10/1/93				50.0	38.0	13.0	63.0	20.0	17.0
10/2/93	18.0	36.0	47.0						
10/29/93	91.0	7.0	2.0	92.0	3.0	5.0			
11/5/93							73.0	23.0	4.0
11/26/93				70.0	27.0	2.0			
11/27/93	78.0	17.0	5.0						
12/3/93							76.0	15.0	9.0
12/29/93				52.0	25.0	23.0	46.0	33.0	21.0
12/31/93	67.0	15.0	18.0						
2/18/94				86.0	3.0	11.0	53.0	36.0	11.0
2/19/94	77.0	18.0	5.0						
3/18/94				90.0	4.0	6.0	84.0	10.0	6.0
3/19/94	88.0	0	12.0						
4/15/94				92.0	3.0	5.0	67.3	10.3	22.4
4/17/94	93.0	2.3	4.6						
5/13/94				78.8	10.4	10.7	71.4	13.9	14.7
5/14/94	88.2	10.0	2.0						
6/17/94				0	49.0	51.0	14.1	8.8	77.1
6/18/94	37.5	30.0	32.5						
7/15/94				16.9	25.4	57.7	30.9	20.1	49.0
7/16/94	15.2	13.1	71.7						
8/19/94				74.4	7.2	18.4	29.9	57.1	13.0
8/21/94	76.9	2.5	20.6						
9/9/94				47.8	33.2	19.0	65.6	20.4	14.0
9/11/94	48.4	21.4	30.2						
10/7/94				16.1	35.8	48.1	49.0	23.9	27.1
10/8/94	18.6	30.6	50.8						
11/4/94				66.4	23.5	10.1	47.3	32.7	20.0
11/5/94	51.8	29.2	19.0						
12/3/94	43.5	30.1	26.4						
12/7/94				58.0	18.3	23.8	56.8	25.9	17.2
1/9/95	73.7	12.8	13.5						
1/10/95				75.6	9.7	14.7	61.2	24.4	14.4
2/17/95				50.9	20.2	28.9	76.5	6.0	17.6
2/18/95	70.6	10.3	19.0						
3/10/95				81.5	9.8	8.8	73.6	11.9	14.5
3/11/95	79.1	7.2	13.6						
4/7/95				74.1	10.7	15.3	5.3	85.7	9.0
4/8/95	61.8	8.2	29.3						
5/5/95				25.4	23.6	51.0	63.4	23.5	13.1
5/6/95	19.9	13.2	66.9						

Table 9. Surface and bottom water mean chlorophyll *a* concentrations and the percentage contribution of each size-fraction to the total chlorophyll during the time when all 3 stations were sampled

	Hammonasset		Milford		Stamford		Trends Between Stations	
	Mean-μgl^{-1}	%TOT	Mean-μgl^{-1}	%TOT	Mean-μgl^{-1}	%TOT	Ham-Mil	Mil-Stam
SURF Ch1	9.9	100	12.8	100	14.5	100	+30%	+14%
BOT Ch1	9.5	100	13.7	100	14.2	100	+44%	+4%
SURF Ch1 >20	5.5	56	8.7	68	9.5	66.0	+58%	+8%
BOT Chl >20	6.1	58	10.0	73	10.3	73.0	+64%	+3%
SURF Ch1 10–20	2.3	23	1.6	13	2.0	14.0	−30%	+25%
BOT Chl 20–20	2.0	21	1.7	12	1.6	11.0	−15%	−5%
SURF Chl <10	2.1	21	2.3	17	2.9	20.0	+10%	+26%
BOT Chl <10	1.4	15	2.0	15	2.4	17.0	+43%	+20%

accuracy of the copepod abundance data was likely compromised now and then.

Intrastation patchiness, based on repeated tows done on 13 occasions, ranged from strong to weak. The data were binned, and this treatment indicated that patchiness was most intense when copepod abundance was 1000–5000 individuals per cubic meter, suggesting that differences between stations would be hardest to detect within that range. In any case, the copepods were usually significantly patchy, and since patchiness data was available for only 13 of 93 samples, comparisons of copepod abundance among stations on individual dates are more-or-less uncertain. Comparing mean abundance among the stations eliminates this problem because every month represents a replicate, and the average implicitely incorporates random errors like those due to patchiness and sampling.

Tests of copepod distribution

Two-way ANOVA (Zar, 1984) was used to test the significance of station location and time of year as factors determining copepod abundance. The data were transformed (natural log), and tested acceptably for normality (Kolmogorov-Smirnoff test p=0.45), and homogeneity of variance (Cochran's C test p=0.51, and Bartlett's test p=0.35), thus meeting the underlying assumptions for ANOVA (Zar, 1984). Station location influenced copepod abundance significantly (p=0.0035). *A posteriori* testing (Zar, 1984) indicated that Hammonasset had fewer copepods than Milford and Stamford ($p \leq 0.05$), while Milford and Stamford were not different. In addition, a nonparametric Kruskall–Wallis test (Zar, 1984) ranked Hammonasset lowest in copepod abundance ($p<0.001$). The seasonal cycle was also significant ($p<0.001$). The data were organized in four seasonal bins (Jan.+ Feb.+ Mar.= winter, and so on), and *a posteriori* testing ranked spring highest in copepods, while summer

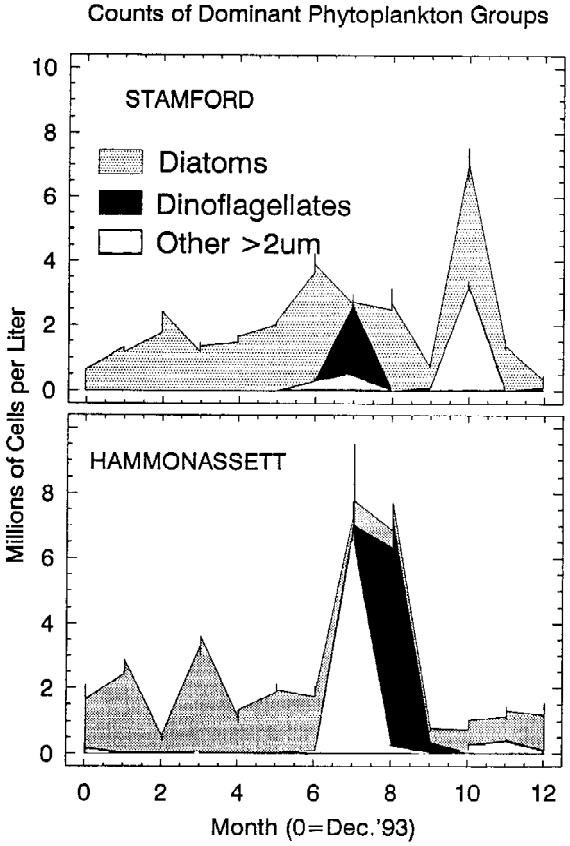


Figure 28. Quantitative counts of dominant phytoplankton by groups (diatoms, dinoflagellates and other greater than 2 μm forms), for the December 1993 to December 1994 sampling period at the Stanford and Hammorasset sites.

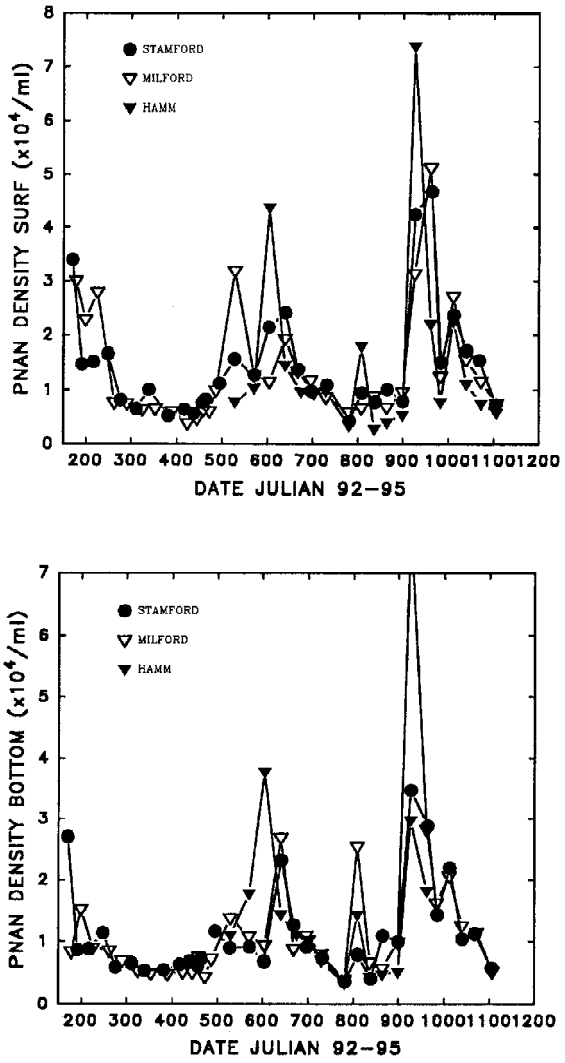


Figure 29. Photosynthetic nanoplankton (PNAN) concentrations for the 3 stations over the entire study period, for surface and bottom waters.

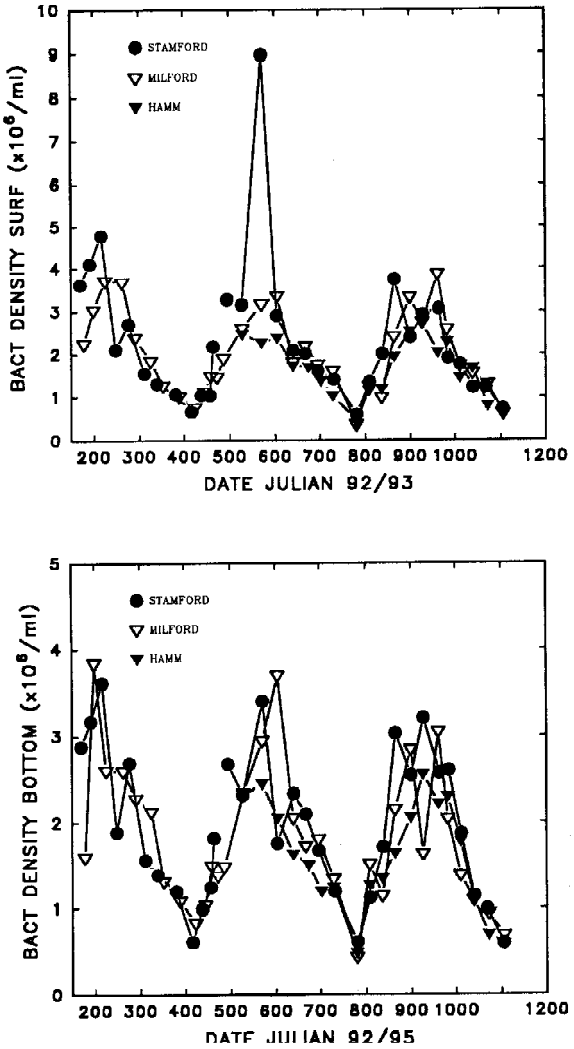


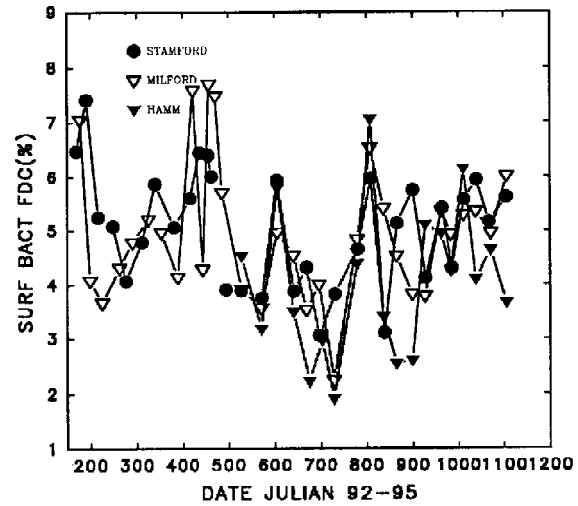
Figure 30. Planktonic bacterial concentrations for the 3 study sites over the entire study period, for surface and bottom waters.

and fall shared lowest rank ($p \leq 0.05$). The interaction between station and season was not significant (p=0.525) even though it appeared that differences among stations were greatest in late spring.

In summary, Hammonasset, the eastern station, had fewest copepods. Spatial gradients seemed less intense during lows in the annual abundance cycle, but interstation comparisons on any given date were suspect because of intrastation patchiness. Nevertheless, when station means were tested, the difference between Hammonasset and the western stations was significant, whereas there was no discernable difference between the two western stations.

Copepod biomass

Not surprisingly, seasonal cycles and spatial trends in copepod biomass (Figs 35 and 36, Table 14) matched well with cycles and trends in copepod abundance. The data suggest an overall increase between Hammonasset and points to the west, and there were high seasonal peaks every spring, most especially in the west. Seasonal variability in biomass became more extreme from east to west, ranging from two to four orders of magnitude at the different stations (Table 14). During spring peaks, there were more of the heavy copepod, *Temora longicornis*, at the western stations, making east–west differences in biomass greater at times than east–west differences based on abundance.



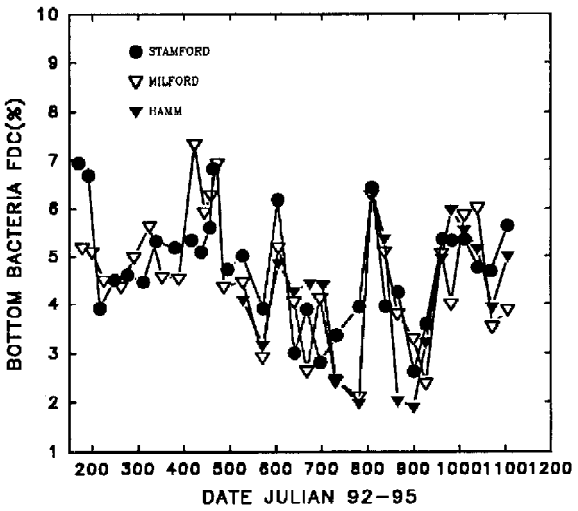
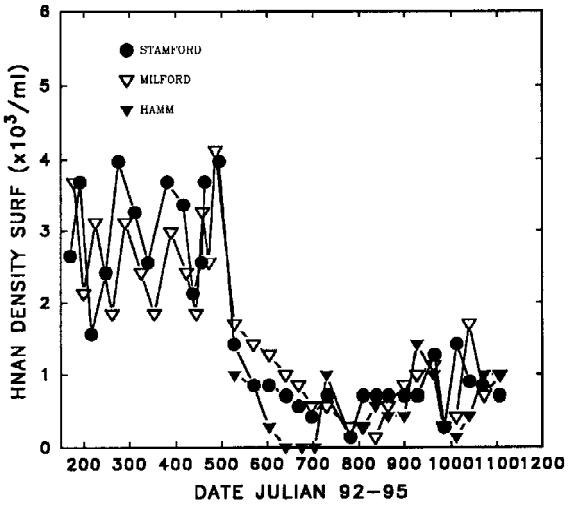


Figure 31. Bacterial growth rates estimated as frequency of dividing cells (FDC), for the 3 sites over the entire study period, for surface and bottom waters.



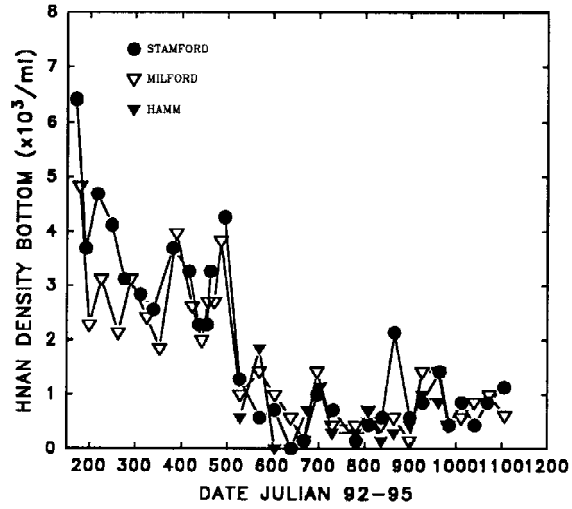


Figure 32. Heterotrophic nanoplankton (HNAN) concentrations for the 3 study sites over the entire study period, for surface and bottom waters.

Conversely, there were instances during seasons of low abundance when Hammonasset had greater biomass, and fewer, heavier, individuals than western stations. In fact, individual *Temora longicornis, Acartia hudsonica,* and *Acartia tonsa* at Hammonasset appeared to weigh 10–20% more on average than they did at Milford and Stamford. This suggests a difference among stations in the age (growth stage) distribution of the copepods within the population.

Tests of biomass distribution

Two-way ANOVA (Zar, 1984) was applied to biomass just as it was to abundance. The data were not normally distributed, so they were transformed (natural log), after which they passed tests for normality (Kolmogorov–Smirnoff test p=0.86), and homogeneity of variances (Cochrans' C test p=0.46, and Bartletts' test p=0.24). Season was a significant influence on biomass ($p<0.001$), and *a posteriori* testing confirmed that biomass was highest in spring ($p<0.05$). During the summer, biomass was generally low, and monthly spatial patterns did not suggest consisten increases from east to west. Differences in mean biomass among stations achieved a significance level approaching 5% (p=0.057) only when the summer data were excluded from the test. *A posteriori* testing confirmed that Hammonasset had less biomass than

Table 10. Phytoplankton species list for all 3 stations for the 1993, 1994, and 1995 study period, indicating the relative abundance as + or ++

Class	Genus	Species	Hammonasset*	Milford	Stamford
1993 Phytoplankton Species List					
Dinophyceae	Amphidinium	sp.			+
Bacillariophyceae	Amphiprora	sp.		++	
Bacillariophyceae	Amphora	sp.	+	+	+
Bacillariophyceae	Asterionella	japonica	+	+	
Bacillariophyceae	Biddulphia	sp.		+	+
Dinophyceae	Ceratium	sp.		+	
Bacillariophyceae	Chaetoceros	affinis	+		+
Bacillariophyceae	Chaetoceros	cuvisetus	++	++	+
Bacillariophyceae	Chaetoceros	danicus		+	
Bacillariophyceae	Chaetoceros	decipiens			+
Bacillariophyceae	Chaetoceros	lorenzianus			+
Bacillariophyceae	Chaetoceros	simplex	+	+	+
Bacillariophyceae	Chaetoceros	tortissimus			+
Chlorophyceae	Chlorella	sp.	+		
Prymnesiophyceae	Coccolithus	huxleyii		+	
Bacillariophyceae	Coscinodiscus	sp.	++	++	+
Chlorophyceae	Cryptomonas	sp.	++	++	
Bacillariophyceae	Cyclotella	cryptica	+	++	
Bacillariophyceae	Detonula	confervaceae	+		+
Silicoflagellate	Dictyocha	sp.			+
Dinophyceae	Dinophysis	acuminata	+	+	+
Silicoflagellate	Distephanus	speculum		++	++
Bacillariophyceae	Ditylum	brightwellii	+	+	+
Bacillariophyceae	Euchampia	zoodiacus	++		++
Euglenophyceae	Euglena	sp.	+		
Bacillariophyceae	Grammatophora	sp.	+	+	
Dinophyceae	Gymnodinium	sanguineum	+	+	
Bacillariophyceae	Gyrosigma	sp.	++		
Bacillariophyceae	Hemiaulis	sinensis	+	+	
Dinophyceae	Heterocapsa	triquetra	+		+
Bacillariophyceae	Heterosigma	sp.			+
Bacillariopnyceae	Leptocylindrus	danicus	++	++	++
Bacillariophyceae	Leptocylindrus	minimum	+	++	++
Bacillariophyceae	Licmophora	sp.			+
Bacillariophyceae	Melosira	sulcata	+	++	++
Bacillariophyceae	Navicula	sp.	++	+	++
Bacillariopjyceae	Nitzschia	closterium		+	
Bacillariophyceae	Nitzschia	longissima	+	+	++
Bacillariophyceae	Nitzschia	seriata	++	++	++
Bacillariophyceae	Nitzschia	sp.	++		+
Dinophyceae	Oxytoxum	sp.		+	
Prymnesiophyceae	Pavlova	sp.	+	+	+
Dinophyceae	Peridinium	sp.		+	
Prymnesiophyceae	Phaeocystus	pouchetti		+	
Dinophyceae	Prorocentrum	micans		+	+
Dinophyceae	Prorocentrum	minimum		++	+
Dinophyceae	Prorocentrum	scutellum	+	+	++
Dinophyceae	Prorocentrum	triestinum		+	+
Dinophyceae	Protroperidinium	sp.		+	+
Prymnesiophyceae	Pyramimonas	sp.	+	+	

Continued on p. 309

Table 10. contd.

Class	Genus	Species	Hammonasset*	Milford	Stamford
Bacillariophyceae	Rhizosolenia	delicatula			++
Bacillariophyceae	Rhizosolenia	faeroense		+	++
Bacillariophyceae	Rhizosolenia	setigera		+	+
Bacillariophyceae	Rhizosolenia	stolterfothii			+
Bacillariophyceae	Skeletonema	costatum	++	++	++
Bacillariophyceae	Stephanopyxix	sp.	+	+	
Prymnesiophyceae	Tetraselmis	sp.		+	
Bacillariophyceae	Thalassionema	nitzschioides	++	+	
Bacillariophyceae	Thalassiosira	decipiens		+	
Bacillariophyceae	Thalassiosira	gravida		+	
Bacillariophyceae	Thalassiosira	nordenskoldii	++	++	++
Bacillariophyceae	Thalassiosira	pseudonana	++	++	++
Bacillariophyceae	Thalassiosira	rotula	++	++	+
Bacillariophyceae	Thalassiothrix	frauenfeldii	++	++	++
Bacillariophyceae	Thalassiothix	longissima	+	+	+
Total number of species by station, 1993			36	48	45
1994 Phytoplankton Species List					
Bacillariophyceae	Achnanthes	sp.	+	+	
Dinophyceae	Amphidinium	sp.	+	+	
Bacillariophyceae	Amphiprora	sp.	+		
Bacillariophyceae	Asterionella	japonica	++	++	++
Bacillariophyceae	Chaetoceros	debilis		+	+
Bacillariophyceae	Chaetoceros	simplex	+	+	
Chlorophyceae	Chlorella	sp.		+	
Prymnesiophyceae	Coccolithus	huxleyii		+	
Bacillariophyceae	Coscinodiscus	sp.	++	+	++
Chlorophyceae	Cryptomonas	sp.	++	++	++
Bacillariophyceae	Detonula	confervaceae			++
Dinophyceae	Dinophysis	acuminata	+		+
Silicoflagellate	Distephanus	speculum		+	
Bacillariophyceae	Ditylum	brightwellii		+	+
Chlorophyceae	Dunaliella	sp.		+	
Bacillariophyceae	Euchampia	zoodiacus		+	++
Euglenophyceae	Euglena	sp.			+
Dinophyceae	Gonyaulax	rotundata			+
Dinophyceae	Gyrodinium	aureolum			+
Bacillariophyceae	Gyrosigma	sp.	++		
Bacillariophyceae	Leptocylindrus	danicus	++	++	+
Bacillariophyceae	Leptocylindrus	minimum	++		++
Bacillariophyceae	Melosira	nummuloides	+		+
Bacillariophyceae	Melosira	sulcata	++	+	+
Bacillariophyceae	Navicula	sp.	++	+	+
Bacillariophyceae	Nitzschia	closterium		+	+
Bacillariophyceae	Nitzschia	longissima	+	+	+
Bacillariophyceae	Nitzschia	seriata	+	+	+
Bacillariophyceae	Nitzschia	sp.	++		
Dinophyceae	Oxytoxum	sp.	++	+	
Prymnesiophyceae	Pavlova	sp.	++		
Dinophyceae	Peridinium	sp.		+	
Prymnesiophyceae	Phaeocystus	pouchettii	++		
Dinophyceae	Prorocentrum	micans		+	+
Dinophyceae	Prorocentrum	minimum		+	+

Continued on p. 310

Table 10. contd.

Class	Genus	Species	Hammonasset*	Milford	Stamford
Dinophyceae	Prorocentrum	scutellum	++	++	++
Dinophyceae	Prorocentrum	triestinum	++		++
Dinophyceae	Protoperidinium	sp.	+	+	
Prymnesiophyceae	Pyramimonas	sp.	+	+	
Bacillariophyceae	Rhizosolenia	delicatula		++	++
Bacillariophyceae	Rhizosolenia	faeroense		++	++
Bacillariophyceae	Rhizosolenia	fragilissima	++		+
Bacillariophyceae	Rhizosolenia	hebetata			+
Bacillariophyceae	Rhizosolenia	setigera		+	
Bacillariophyceae	Skeletonema	costatum	++	++	++
Bacillariophyceae	Thalassionema	nitzschioides		+	++
Bacillariophyceae	Thalassiosira	nordenskoldii	++	++	++
Bacillariophyceae	Thalassiosira	pseudonana	++	++	
Bacillariophyceae	Thalassiosira	rotula	++	++	+
Bacillariophyceae	Thalassiothrix	frauenfeldii	++	++	++
Total number of species by station, 1994			32	35	33
1995 Phytoplankton Species List					
Dinohyceae	Amphidinium	sp.			+
Bacillariophyceae	Amphiprora	sp.	+		
Bacillariophyceae	Asterionella	japonica		+	
Dinophyceae	Ceratium	sp.	+		
Bacillariophyceae	Chaetoceros	simplex			+
Bacillariophyceae	Coscinodiscus	sp.	+	+	++
Chlorophyceae	Cryptomonas	sp.	+	+	++
Bacillariophyceae	Detonula	confervaceae			++
Dinophyceae	Gonyaulax	rotundata		++	
Dinophyceae	Gymnodinium	sanuineum	+		
Bacillariophyceae	Gyrosigma	sp.	+		+
Dinophyceae	Katodinium	rotundatum		+	
Bacillariophyceae	Leptocylindrus	danicus	++	++	++
Bacillariophyceae	Leptocylindricus	minimum	++		
Bacillariophyceae	Melosira	sulcata	++	++	++
Bacillariophyceae	Navicula	sp.		+	
Bacillariophyceae	Nitzschia	sp.		+	+
Dinophyceae	Prorocentrum	scutellum			+
Dinophyceae	Protoperidinium	sp.	+	++	++
Prymnesiophyceae	Pyramimonas	sp.		++	
Bacillariophyceae	Rhizosolenia	faeroense	++		
Bacillariophyceae	Rhizosolenia	fragilissima	++	++	++
Bacillariophyceae	Skeletonema	costatum	++	++	++
Prymnesiophyceae	Tetraselmis	sp.			++
Bacillariophyceae	Thalassionema	nitzschioides	++	++	++
Bacillariophyceae	Thalassiosira	decipiens			++
Bacillariophyceae	Thalassiosira	nordenskoldii	+	++	++
Bacillariophyceae	Thalassiosira	pseudonana		++	++
Bacillariophyceae	Thalassiosira	rotula	++	++	++
Bacillariophyceae	Thalassiothrix	frauenfeldii	++		+
Total number of species by station, 1995			17	18	22

*Sampled only 6 months.

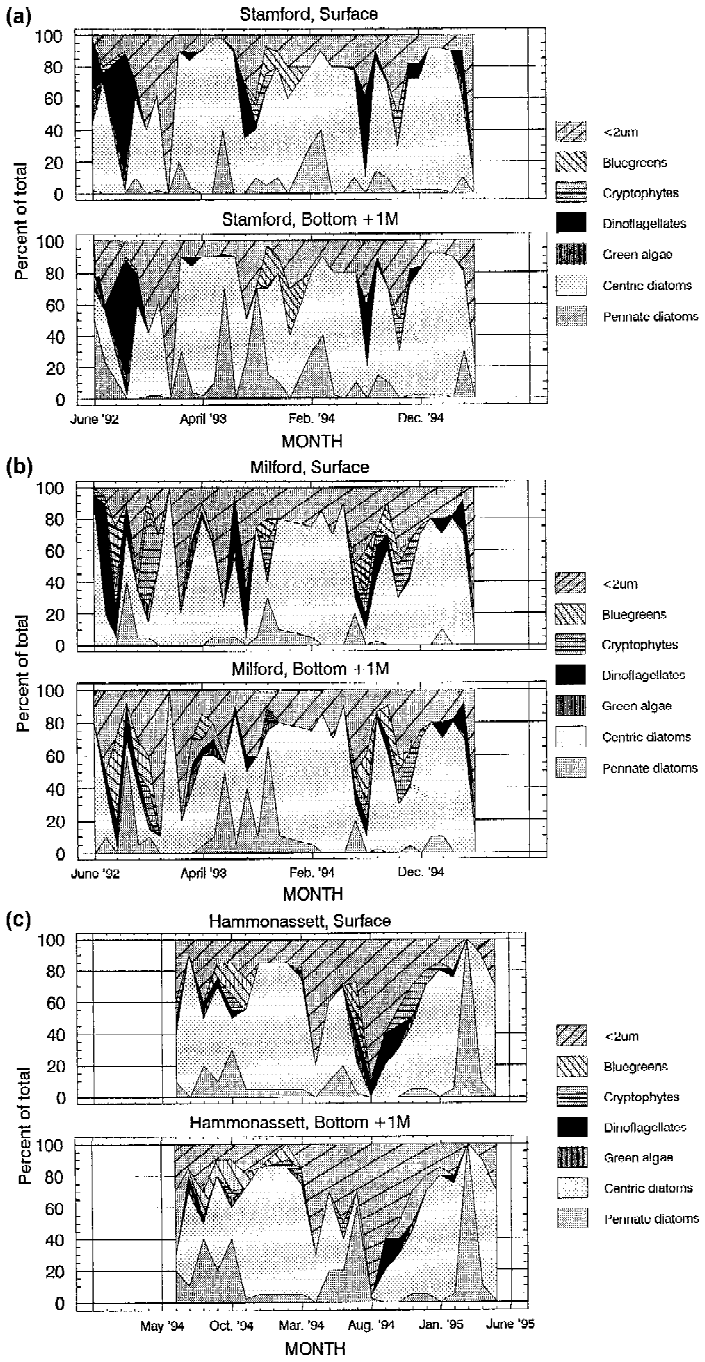


Figure 33. The percentage of phytoplankton assemblages in major taxonomic groups for the surface and bottom waters of all 3 study sites over the entire study period.

the western stations during spring, fall, and winter ($p \leq 0.05$). Milford ranked lowest during summer based on a nonparametric Kruskal–Wallis test (p=0.023), whereas Hammonasset ranked lowest the rest of the year (p=0.021).

In summary, the dominant pattern of biomass was an increase between Hammonasset and the western stations. The increase appeared especially strong in the spring, and it also prevailed in fall and winter. Gradients became variable and uncertain in the summer.

Table 11. Complete planktonic ciliate species composition list for the entire study period, for the 3 Long Island Sound study sites combined, based on protargol stained specimen analyses

Ciliate species list for all stations combined		
Codonellopsis sp.	*S. ventricosa*	*S. taylori*
Codinella sp.	*Strobilidium elegans*	*S. Titinnodes*
Cyrtostrombidium longisomum	*S. epacrum*	*S. tressum*
C. wailesi	*S. marinum*	*S. ventropinnum*
Didinium sp.	*S. multinucleatum*	*Tetraphyminid scutico*
Euplotes sp.	*S. spharicum*	*Tintinnopsis acuminata*
Eutintinnus pectinis	*S. spiralis*	*T. baltica*
E. lusundae	*S. undinum*	*T. beroidea*
Favella arcuata	*S. veniliae*	*T. dadayi*
F. ehrenbergii	*Strombidinopsis cheshira*	*T. fluviatile*
F. sp.	*S. multiauris*	*T. kofoidi*
Haltera sp.	*Strobidium acuminatum*	*T. levigata*
Helicostomella subulata	*S. acutum*	*T. minuta*
H. ssp.	*S. basimorphum*	*T. parva*
Heterotricous condilostima	*S. bilobum*	*T. platensis*
Laboea strobila	*S. capitatum*	*T. rapa*
Leegardiella sol	*S. compressum*	*T. tubulosa*
Lohmanniella oviformis	*S. conicum*	*T. tubulosoides*
Mesodinium sp.	*S. daparedei*	*T. urnula*
Metacylis angulata	*S. inclinatum*	*T. vasculum*
M. annulifera	*S. lynni*	*T. ventricosoides*
Metastrombidium p.	*S. pelagicum*	*Tontonia gracillima*
Stenosemella oliva	*S. siculum*	*T. poopsia*
S. steini	*S. sulcatum*	

Table 12. Numbers and percentages of ciliate species encountered over the entire study period, for the entire study area, and by station, both as averages for the entire water column and by depth

Site	# of species	% of total	% in surface waters	% in bottom waters
Σ of all sites	71	100	–	–
Stamford site	67	94	72	69
Milford site	57	80	58	63
Hammonasset site	44	62	54	45

Species composition of the copepods

Results are presented for eight of the copepod species that were identified and enumerated. A ninth species will be mentioned in passing. All were observed at one time or another at each station (Table 15). Two major subgroups were noted; one comprising three species dominated the winter and spring seasons, and the other, with four species, dominated the summer and fall seasons. They typically overlapped briefly twice a year. From December through June (winter–spring season) *Acartia hudsonica* and *Temora longicornis* (Fig. 37) were predominant, and *Pseudocalanus* sp. was present in lower numbers (Fig. 38). *Centropages* sp. occurred during the spring and the summer (Fig. 38), but its numbers were low. From July through December (summer–fall season), *Acartia tonsa* usually dominated, and *Paracalanus crassirostris* could be abundant, especially during the fall (Fig. 39). There were two other summer–fall species, *Oithona* sp., and

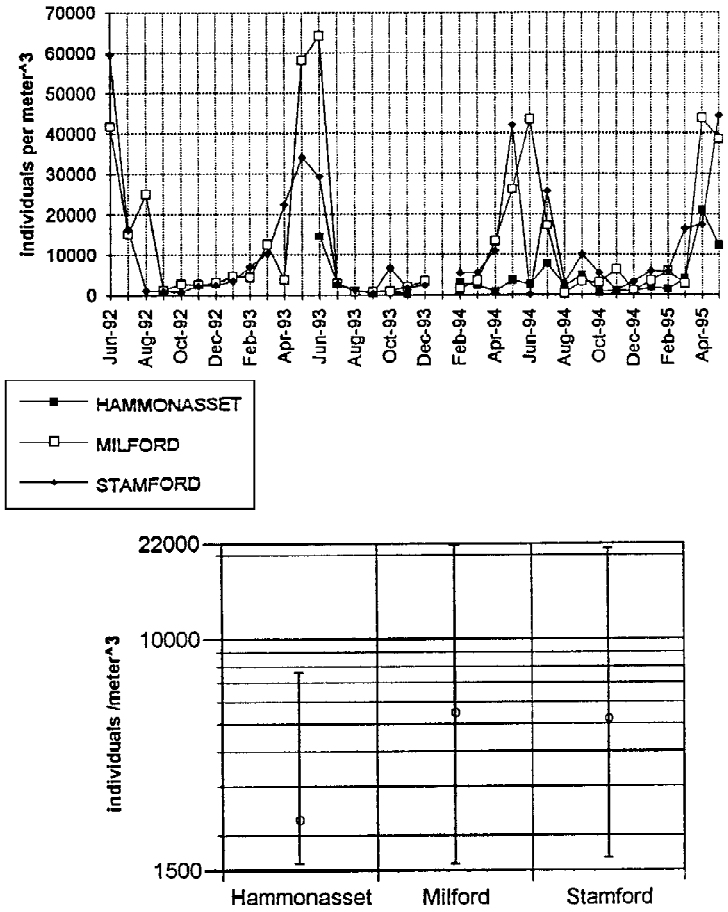


Figure 34. Number of copepods per m^3 (top), and the geometric means and standard deviations of copepod abundance (bottom) for the entire study period, averaged for the water column.

Labidocera sp. (Fig. 40), found in lesser numbers. A ninth species, *Eurytemora hardmanni*, was observed in insignificant numbers (2–4 copepods m^{-3}) in the spring. The seasonal species succession was well synchronized at all stations, and it was much the same from year-to-year for all of the dominant copepods (Fig. 41).

Patterns of the species among stations

Species composition was similar at each station, except that *Temora longicornis* was slightly more dominant at the two western stations during the winter and spring, and *Acartia tonsa* was slightly more dominant at the center station (Milford) in the summer and fall (Table 15). When all copepods were tallied over the period of study, 85% belonged to winter–spring varieties at Milford and Stamford, whereas the counts were somewhat more evenly divided between winter–spring and summer–fall varieties at Hammonasset (Table 15). One genus, *Centropages* sp., actually decreased from east to west, but this was one of the less abundant copepods. *Centropages typicus* and *Centropages hamatus* were considered by Deevey (1956) as primarily neritic (or less tolerant of reduced salinity), possibly explaining their distribution.

In summary, nine species were identified and counted, and all were present at each station. There were two major subgroups, winter–spring (boreal), and summer–fall (warm water). In winter and spring, *Temora longicornis* and *Acartia hudsonica* were numerically dominant. In summer and fall, *Acartia tonsa* and *Paracalanus crassirostris* were numerically dominant. There was no striking difference among stations in the species compostion of the copepod

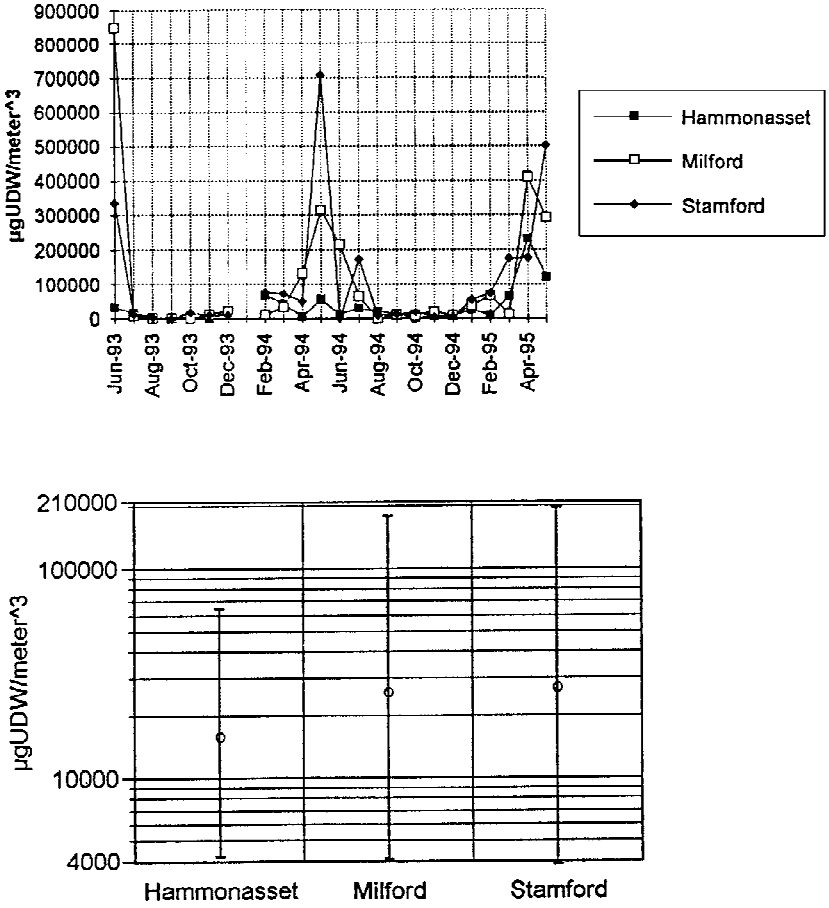


Figure 35. Combined biomass of the copepods *Temora longicornis,/ Acartia hudsonica* and *Acartia tonsa* (top), and the geometric means and standard deviations of biomass (bottom) for the entire period of study (values are water column integrated averages), presented as unpreserved dry weight (UDW).

Table 13. Descriptive statistics of copepod abundance for the period of the study

	Numbers of individuals per m^3		
	Hammonasset	Milford	Stamford
Mean	4162	13 288	11 677
Geometric mean	2303	5548	5282
Minimum	361	415	183
Maximum	21 053	64 152	59 542
Standard deviation around the mean	±5301	±17 793	±14 535
Standard deviation around the geometric mean	+5527 −717	+16 065 −3967	+15 721 −3620

Table 14. Descriptive statistics for the combined biomass of 3 major copepod species, *Temora longicornis, Acartia hudsonica*, and *Acartia tonsa*, over the period of study in units of unpreserved dry weight (UDW)

	μg UDW/m^3		
	Hammonasset	Milford	Stamford
Mean	36 217	110 715	109 229
Geometric mean	16 103	26 213	27 535
Minimum	1 765	1 036	405
Maximum	223 775	847 554	707 655
Standard deviation around the mean	±53 180	±198 365	±179 214
Standard deviation around the geometric mean	+48 546 −11 903	+152 597 −22 123	+168 490 −23 671

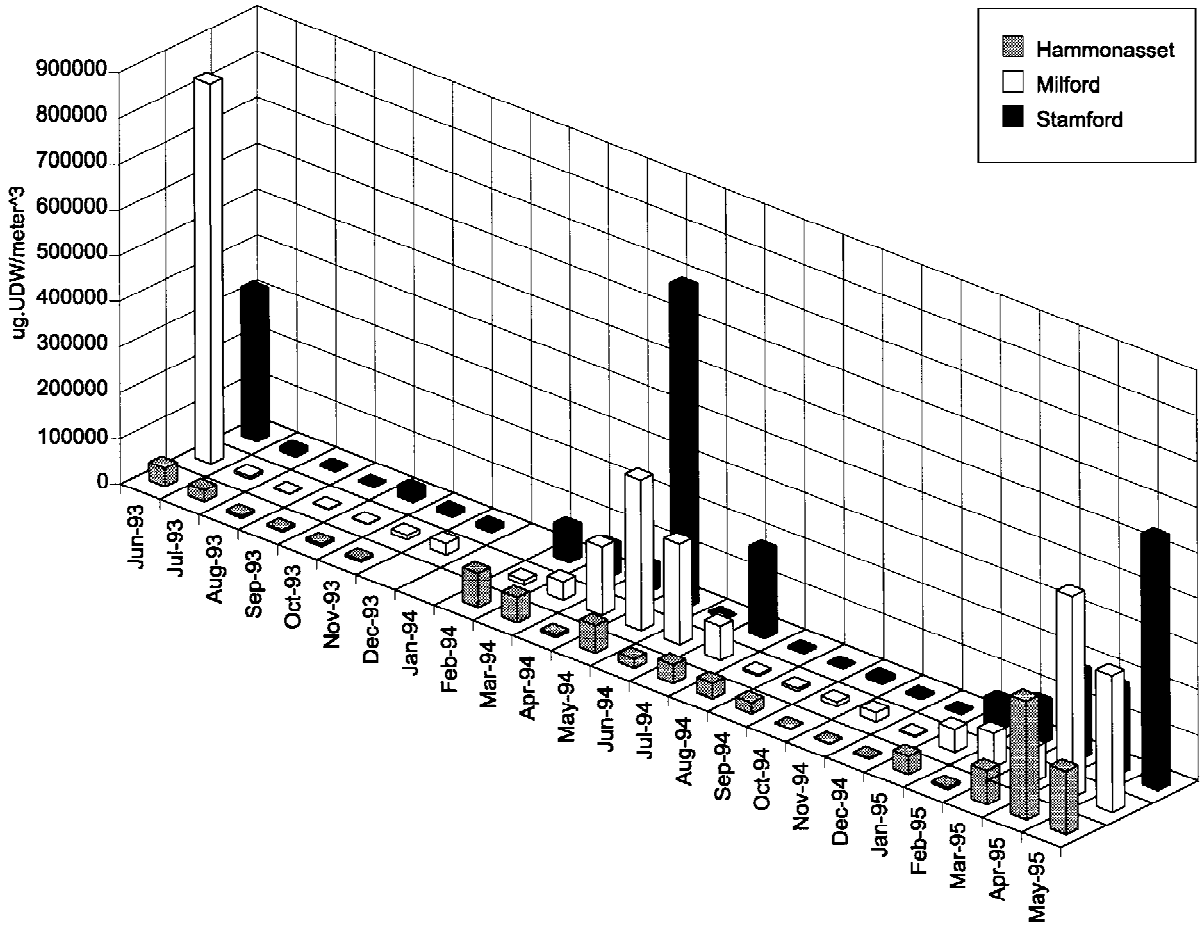


Figure 36. Copepod biomass, as μg unpreserved dry weight (UDW)/m^3) by station. In the entire period of study (values are water column integrated averages).

community. However, over the period of study most of the copepods in the west occurred in the winter–spring assemblage due to massive springtime populations, while at Hammonasset they were more evenly divided between winter–spring and summer–fall assemblages.

Correlations between copepod data & other variables

Seasonal patterns of copepod abundance and (or) biomass correlated positively with Chl and (or) Chl >20 at all three stations. Moreover, stations with more chlorophyll and Chl >20 had more copepods, thus copepods and chlorophyll appeared to associate spatially with one another along the eutrophication gradient. There were no correlations between copepods and Chl 10–20 or Chl <10. Copepod numbers and (or) biomass were correlated negatively with DIN and NO_x concentrations at two of three stations, which was due to very low NO_x concentrations during the peaks in copepods. The overall increase in copepods took place between Hammonasset and Milford, whereas a small increase in DIN occurred between Milford and Stamford, thus there was no strong spatial association between DIN concentration and copepods along the eutrophication gradient. Chl and Chl >20 concentrations were negatively correlated with DIN and NO_x concentrations, and positively correlated with PN concentrations, suggesting the uptake of DIN by algae and conversion to PN.

Dissolved inorganic nitrogen concentrations were negatively correlated with PN and DON concentrations, implying seasonal trade-offs between inorganic and organic forms of nitrogen. Correlations of TDN concentrations with DIN concentrations as well as DON concentrations suggest that control of TDN levels can lie with either DIN or DON. Correlations of TN levels with TDN concentrations as well as PN con-

Table 15. Means of copepod abundance by species in units of ind/m^3; relative proportions of each species, as pecentage, for winter–spring, or summer–fall copepod populations, and relative proportion of all the copepods, counted over the period of study, occurring in the winter–spring and summer–fall subgroups

	Hammonasset		Milford		Stamford	
	X	%	X	%	X	%
Winter–Spring Copepod Group						
Temora longicornis	868	29	4431	40	3623	37
Acartia hudsonica	2070	69	6422	59	5972	62
Pseudocalanus sp.	61	2	117	1	91	1
Summer–Fall Copepod Group						
Acartia tonsa	895	74	1680	85	1438	74
Paracalanus sp.	287	24	245	12	475	24
Oithona sp.	17	1.5	35	2.5	33	1.7
Labidocera sp.	8	0.5	8	0.5	5	0.3
A Genus Present Mostly in Spring–Summer						
Centropages sp.	89		56		14	
Relative Proportions of the Winter–Spring and Summer–Fall Groups within the Overall Population						
Winter–Spring		70		85		84
Summer–Fall		30		15		16

centrations suggest that control of TN levels is shared between dissolved and particulate forms of nitrogen.

Copepods are an important part of the food web in LIS, and their seasonal and spatial distributions can be influenced by the quantity and quality of phytoplankton, as well as by water temperature and predation. The distribution of phytoplankton may in turn be influenced by the quantity and chemical composition of dissolved nitrogen, among other things. Therefore, a eutrophication gradient in LIS appears to influence the spatial distribution of copepod populations.

Zooplankton other than copepods

The zooplankton focused on in this study were the protozooplankton and the microcrustaceans (i.e. the copepods). We did, however record all non-copepod macrozooplankton encountered in our sub-samples. Since our sub-sampling was designed to quantify the copepods, we often encountered too few 'other zooplankton' to come up with reliable quantitative estimates. We did, nonetheless, note their presence or absence as ecological functional groups. Some seasonal patterns appear in certain of the larval groups and in the gelatinous depris, which is most common in the summer and fall sampling periods. Of particular noteworthness is the fact that gelatinous zooplankton wet volumes, primarily derived from ctenophores bodies, appears to be much more prevelant at our western Long Island Sound Stamford station.

Larval fish species composition & densities

In all, over the 3 years of study (1992–1995), 18 species of larval fish were encountered and ranked according to abundance, at our 3 Long Island Sound inshore stations (Table 16). The number of species encountered on any sampling date varied from 0 to 6 (Figs 42 and 43) with densities varying from 0 to a high of 120 per cubic meter (Figs 44 and 45). Similar trends in diversity as well as abundances were observed at all 3 stations. When differences were observed they typically were minimal, with Stamford, CT waters having higher concentrations. The 18 species encountered in this study compares to 22 species observed by S. Richards (Riley, 1955; Riley et al., 1956) in her 1952–1955 data set. Comparison of the 1950s and 1990s data indicates that 15 larval fish species were common to both data sets. Three species were found in the present study but not in the 1950s samples (Table 17), and 7 species were observed in the 1950s samples but not in our 1990s data set (Table 18). It is of particular interest that most of the species missing in the current study are species that have either experienced intensive fishing pressure (e.g. 4-Spotted and Yellowtail Flounder, Sea Robins), predator-induced mortality from estuary-feeding birds such as cormorants, or hypoxia stress (e.g. Atlantic Silverside).

Discussion

The various agents of eutrophication affecting Long Island Sound have only slightly elevated levels of dissolved nitrogen compounds, and more significantly enhanced dissolved phosphate levels in Long Island Sound (primarily in the western portions of the estuary. Nitrate and nitrite concentrations throughout the Sound are similar in concentration to those reported in the 1950s by Riley (1955) and Riley et al. (1956). The relative proportioning among chemical species of nitrogen, however, differs from west to east, both contemporaneously, as well as temporally, with NH_4 and dissolved organic nitrogen at times more prevalent in the west (particularly in bottom waters). The excess loadings of nitrogen, and other nutrients into the western Sound appear to be taken up by the planktonic

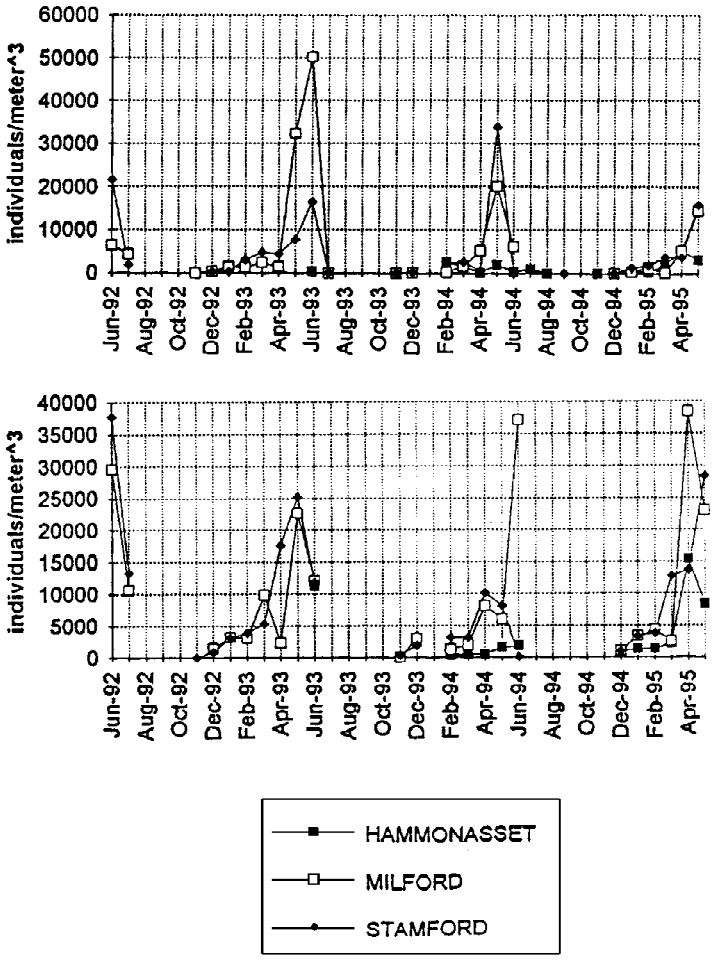


Figure 37. Abundance of individual copepods of the species *Temora longicornis* (top) and *Acartia hudsonica* (bottom), for the entire study period (values are water column integrated averages).

food web and converted to biomass as evidenced by observed bacterial, chlorophyll, phytoplanktonic and zooplanktonic west to east concentration gradients. Size-fractionated chlorophyll data indicate little east to west differences in the 10–20 μm size fraction, while pointing to large differences in the <10 and >20 μm fractions, which are both higher in the west. Occurring along with the enhanced phytoplankton biomass is slightly enhanced bacterial densities and growth rates. The densities show interesting seasonal cycles and appear to be related not to total chlorophyll levels but to densities of the photosynthetic nanoplankton. Heterotrophic nanoplankton densities are also higher in the west and appear also to at times influence bacterial densities.

Species composition of phytoplankton routinely differ among west to east stations. These species compositional shifts appear to be related to N/P and N/Si ratios, as well as to ratios among nitrogen chemical species. Dissolved inorganic N/P ratios are routinely low among all stations , with the west exhibiting lower levels than the east. However, total dissolved N/P ratios (which include dissolved organic nitrogen) are similar among stations and typically are well above the Redfield ratio of 16:1.

Associated with enhancement of bacterial, HNAN and <10 μm chlorophyll is significant enhancement of planktonic ciliate species diversity in the western Long Island Sound waters.

Microcrustacean (i.e. copepod) biomass is extremely enhanced in the west *versus* the east, indicating that while stimulating the microbial loop, eutrophication is also enhancing secondary production preferred by larval fish, comb jellies and jellyfish.

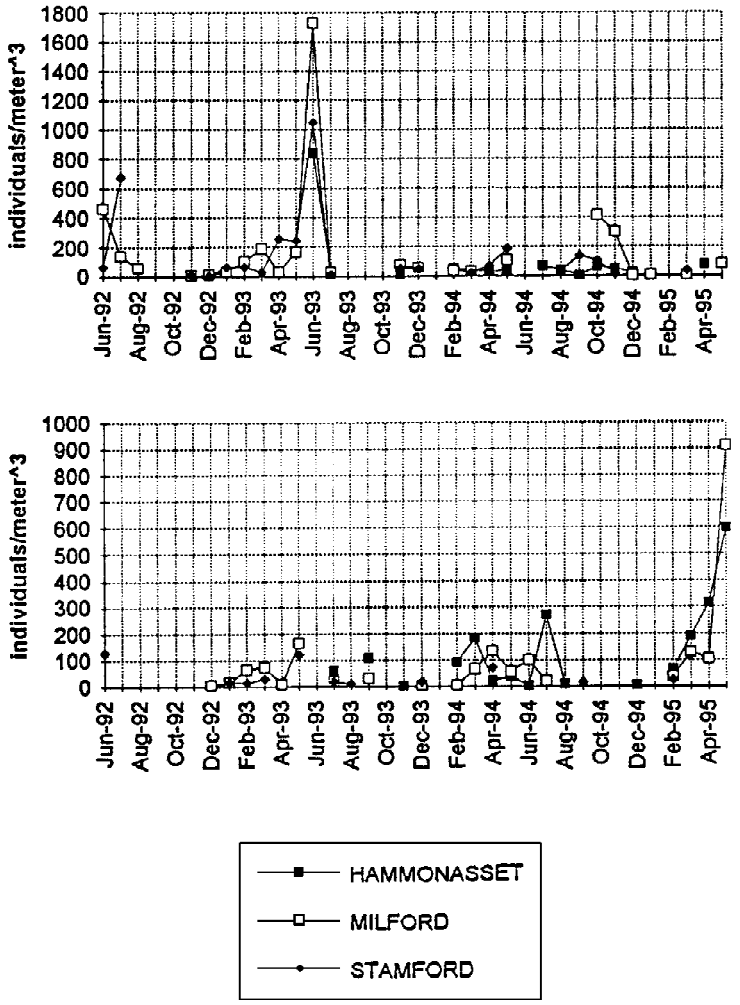


Figure 38. Abundance of individual copepods of the species *Pseudocalanus* sp. (top) and *Centropages* sp. (bottom); for the entire study period (values are water column integrated averages).

Copepod biomass as well as fecal pellet production likely is a significant contributor to hypoxia formation in western Long Island Sound. Copepods increased in number and biomass between the eastern station at Hammonasset, and the two western stations at Milford and Stamford, particularly in the spring. In addition, the spatial pattern of copepod stocks matched best with the spatial pattern of large-size phytoplankton (Chl >20), as opposed to any of the other chlorophyll or nitrogen parameters that were measured. Moreover, the seasonal cycles of copepods, chlorophyll, and nitrogen were in good general agreement with the overall scheme for LIS in the literature, with certain exceptions: (1) High winter NO_x levels lasted longer, until March or even April, although peaks were similar in height. (2) Flowerings during the winter–spring period peaked in March or April, rather than February or March. (3) Chlorophyll levels were higher on average, and particularly so in summer. (4) Spring peaks in copepods were lower than expected at Hammonasset. (5) The summer–fall copepods did not achieve population levels as high as expected. These differences could be due to offshore-inshore gradients, and (or) spatio-temporal changes brought about by eutrophication. Copepod abundance and biomass increased between the eastern station and the central station, but not between the central station and the western station. Events in the temperature cycle, the copepod abundance cycle, and the species succession occurred simultaneously at all three stations, which argues that temperature affected the copepods seasonally, but not spatially. The greatest spatial increases in copepods

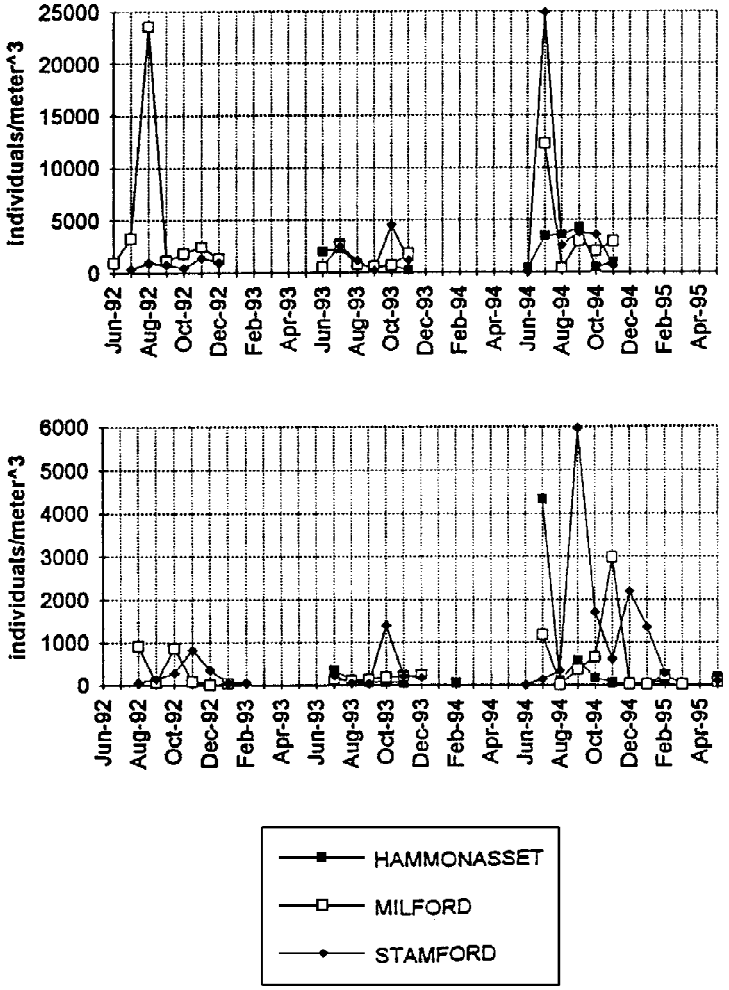


Figure 39. Abundance of individual copepods of the species *Acartia tonsa* (top) and *Paracalanus crassirostris* (bottom) for the entire study period (value are water column integrated averages).

took place in the spring, and a difference in the food supply among stations could be responsible.

Yearly differences in the characteristics of the peak in winter–spring copepods seem to correspond to characteristics of the winter–spring bloom (Harris & Riley, 1956; Harris, 1959; Dam, 1989). This leads to suspicion that spatial differences in the characteristics of the blooms might correspond to spatial differences in the copepods, and there is some evidence of this. Peak populations of winter–spring copepods followed peak concentrations of Chl >20, and peaks in copepods as well as in Chl >20 lasted longer at Milford and Stamford than they did at Hammonasset (Fig. 46). Moreover, the east–west trends in copepod standing stocks and the east–west trends in Chl >20 were similar in size and direction (Fig. 47). In addition, copepod standing stocks and Chl >20 were significantly correlated to each other at all stations.

Strong patterns of east–west increase in the abundance of the boreal copepods gave way in summer to much weaker east–west patterns in the abundance of the warm-water copepods. Conover (1956) suggests that the seasonal switches between boreal and warm-water copepods involve temperature dependent competitive interactions of special importance to fecundity and juvenile growth, more than lethal effects. Boreal species receded rapidly when temperatures increased to 18–20 °C, and the tropical species gave way more slowly when temperatures decreased again to 15–10 °C. The peak populations of winter–spring copepods in May and June collapsed, as expected, when water temperatures began to exceed 18 °C, but the summer–

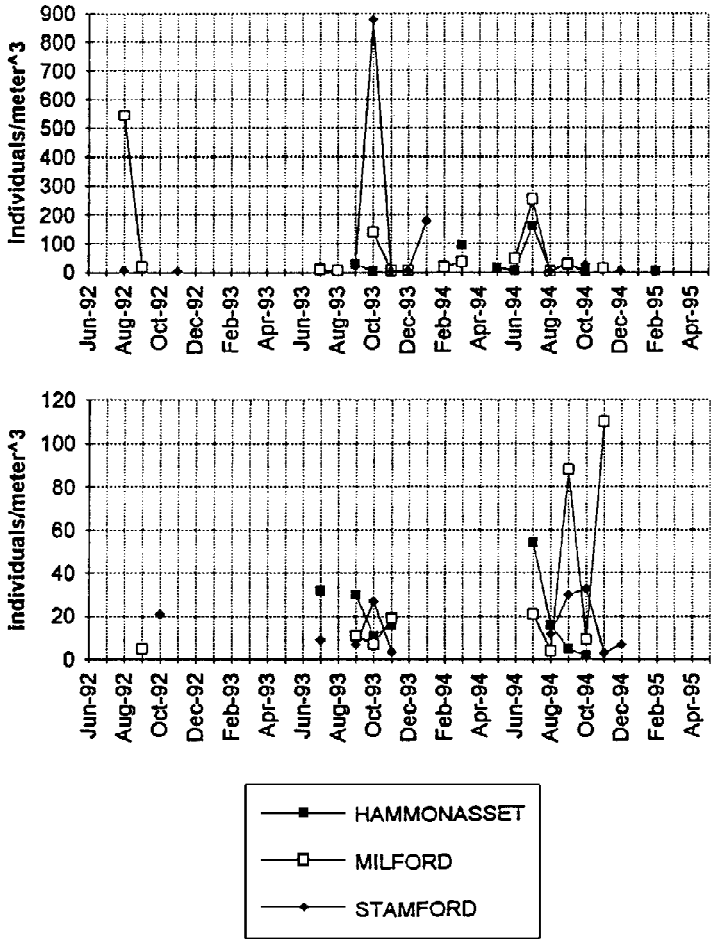


Figure 40. Abundance of individual copepods of the species *Oithona* sp. (top) and *Labidocera* sp. (bottom) for the entire study period (values are water column integrated averages).

fall varieties replacing them never achieved similarly high population levels. Copepod stocks were uniformly low in summer and fall, with only two notable exceptions. One exception was in July 1994, when copepods peaked at all three stations, and the other was in August 1992 only at Milford. Copepods did not appear to be food limited (based on our unpublished data and a food limitation model not presented here) in summer on an assumed diet of Chl >20, and as mentioned above, there is little question that the likelihood of food limitation was reduced even further by omnivory.

Circumstantial evidence implicates ctenophores in controlling the abundance of the summer–fall copepods. In summer and fall of 1992, 58% of zooplankton samples held ctenophore debris (ctenophores preserve very poorly in formalin). In summer and fall of 1993, 45% of zooplankton samples held ctenophore debris. In summer and fall of 1994, however, ctenophore debris occurred in only 27% of zooplankton samples, and 1994 saw the occurrence of a peak in standing stocks of summer–fall copepods at all three stations. Predation rates of 20–100% d^{-1} by seasonal ctenophore swarms on copepods have been noted to occur in various northeast estuaries (Bishop, 1967; Kremer, 1979; Johnson, 1987). Johnson (1987) also noted an inverse relationship between numbers of ctenophores and numbers of copepods.

The east–west trends of increase in nitrogen concentrations were much weaker than the east–west trends of increase in both chlorophyll concentrations and copepod abundance. The DIN fraction was usually slightly more concentrated west of Hammonasset in the winter, which may have had something to do with the east–west patterns of chlorophyll and copepods in the spring. Nitrogen loading and primary produc-

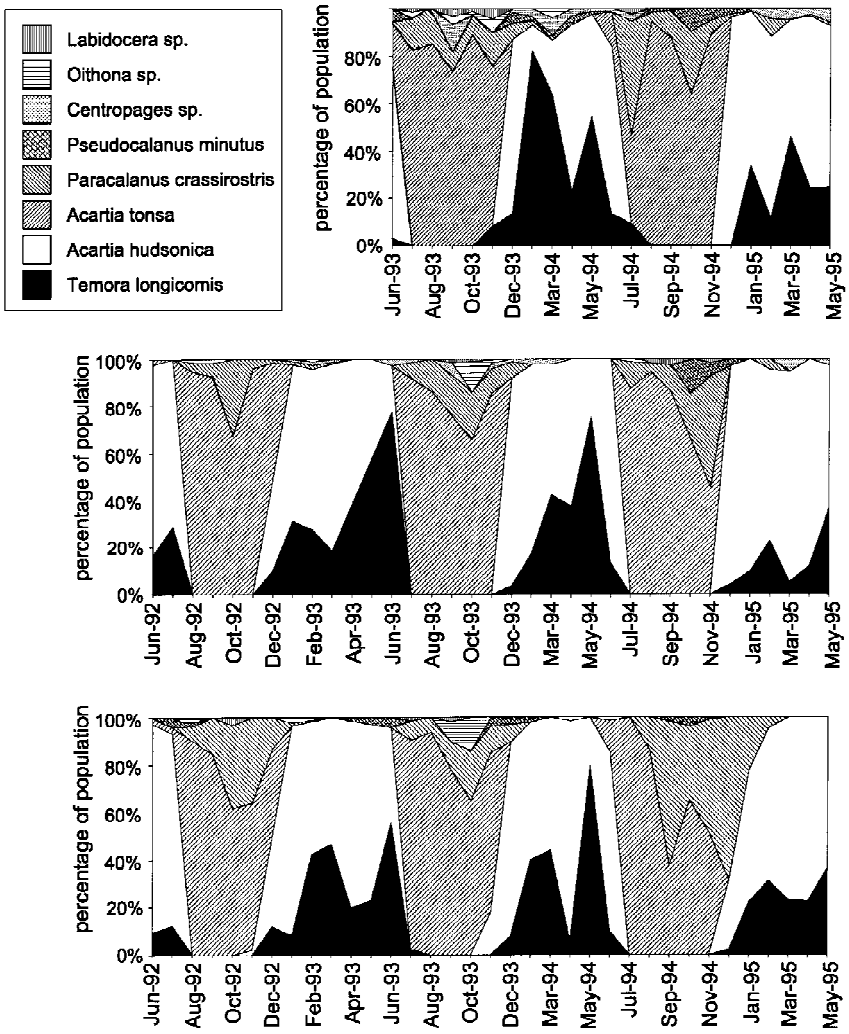


Figure 41. Species composition of the water column copepod populations at the Hammonasset (top), Milford (center) and Stamford (bottom) stations for the entire period of study.

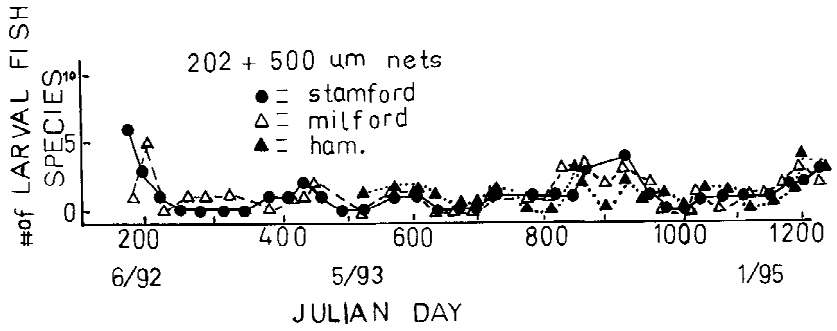


Figure 42. Number of larval fish species encountered at each of the 3 stations for the 202 μm and 500 μm combined water column net samples, over the entire study period (expressed as Julian days, commencing on January 1, 1992).

Table 16. Larval fish species encountered in our inshore Long Island Sound waters, and the abundance ranking for each (1992 – 1995)

Common name	Larval Fish Species Encountered 1992–1995 Inshore Long Island Sound Waters Genus & species	Abundance ranking
Wry Mouth	*Cryptocanthodes maculatus*	12
Butterfish	*Peprilus triacanthus*	10
Pipefish	*Syngnathus fuscus*	10
Windowpan Flounder	*Scophthalmus aquosus*	9
Four-bearded Rockling	*Enchlopus cimbrius*	8
18-spine Sculpin	*Myoxocephalus octodecemspinosus*	7
Tautog (Blackfish)	*Tautoga onitis*	6
Menhaden	*Brevoortia tyrannus*	5
Cunner	*Tautogolabrus adspersus*	4
Winter Flounder	*Pseudopleuronectes americanus*	3
Sand Lance	*Ammodytes americanus*	2
Anchovy	*Anchoa mitchilli*	1
Herring	*Clupea harengus*	Occasional
Cod	*Gadus morhua*	Occasional
Little Sculpin	*Myoxocephalus aeneus*	Occasional
Scup (Porgy)	*Stenotomus chrysops*	Occasional
Hogchocker	*Trinectes maculatus*	Occasional
Sea Snail	*Liparis liparis*	Occasional

Table 17. Larval fish species encountered in the present study (1992–1995), but not found in S. Richards (Riley et al., 1956, 1959) 1952–1955 work

Common name	Larval Fish Species Encountred in the Present Study (1992–1995) but not found in S. Richards (Riley et al. 1955) 1952–1955 work Genus & species
Wry Mouth	*Cryptocanthodes maculatus*
Hogchocker	*Trinectes maculatus*
Sea Snail	*Liparus liparus*

Table 18. Larval fish species encountered in S. Richards (Riley et al., 1956, 1959) work for 1952–1955, but not found in the present study (1992–1995)

Common name	Larval Fish Species Encountered by S. Richards (Riley et. al., 1955) for 1952–1955, but not Found in the Present 1992–1995 Study Genus & species
Atlantic Silverside	*Menidia menidia (notata)*
Northern Kingfish	*Menticirrhus saxatilis*
Northern Sea Robin	*Prionotus carolinus*
Striped Sea Robin	*Prionotus evolans*
4-Spotted Flounder	*Paralichthys oblongus*
Yellowtail Flounder	*Limanda ferruginea*
Northern Puffer	*Sphaeroides maculatus*

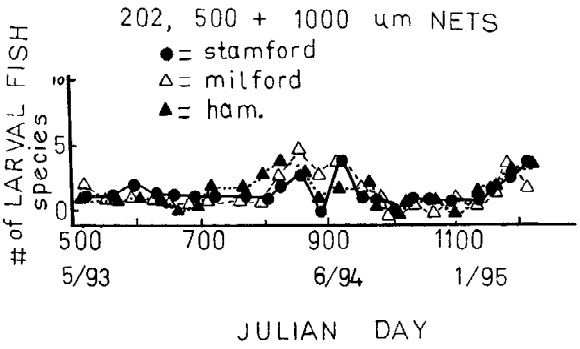


Figure 43. Number of larval fish species encountered at each of the 3 stations for the 202 μm, 500 μm and 1000 μm combined water column net samples, over the entire study period (expressed as Julian days).

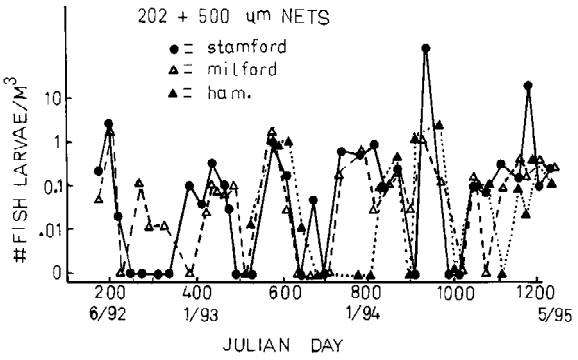


Figure 44. Number of larval fish/m^3 at each of the 3 stations for the 202 μm and 500 μm combined water column net samples, over the entire study period (expressed as Julian days).

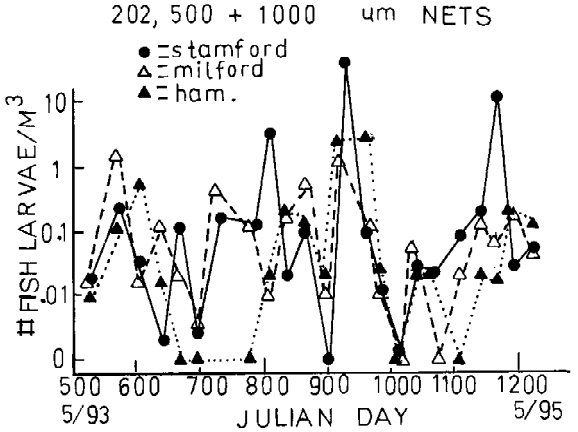


Figure 45. Number of larval fish/m3 at each of the 3 stations for the 202 μm, 500 μm, and 1000 μm combined water column net samples, over the entire study period (expressed as Julian days).

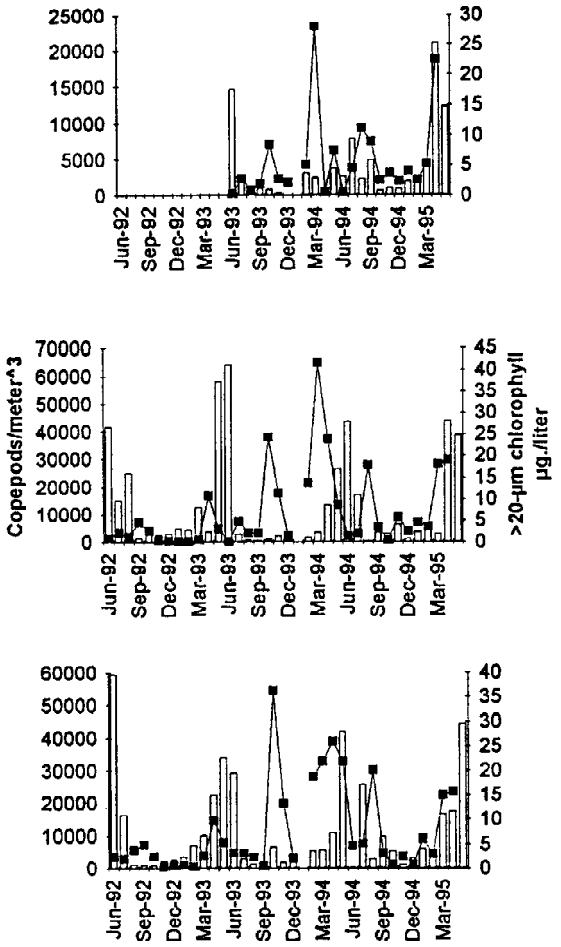


Figure 46. Copepod abundance (as histograms) and depth-averaged greater than 20 μm chlorophyll (line graphs), at the Hammonasset (top), Milford (center), and Stamford (bottom) stations.

tion were well correlated in three of four estuaries studied by de Jonge et al. (1995), including LIS; leading one to conjecture that primary production rates may act to buffer nitrogen concentrations in such a way that regional differences in nitrogen loading do not cause proportional regional differences in nitrogen concentration. It could also be suggested that grazers buffer chlorophyll concentrations, only not as well as primary production buffers nitrogen; perhaps explaining why small east–west increases in nitrogen were associated with larger increases in chlorophyll, and even larger increases in copepods. The occurence of top-down-control over standing stocks in food webs has been noted (see reviews by Carpenter et al., 1985; McQueen et al., 1989; Hunter & Price, 1992; Power, 1992; Strong, 1992). Thus, the large east–west increase in the winter–spring copepod population is

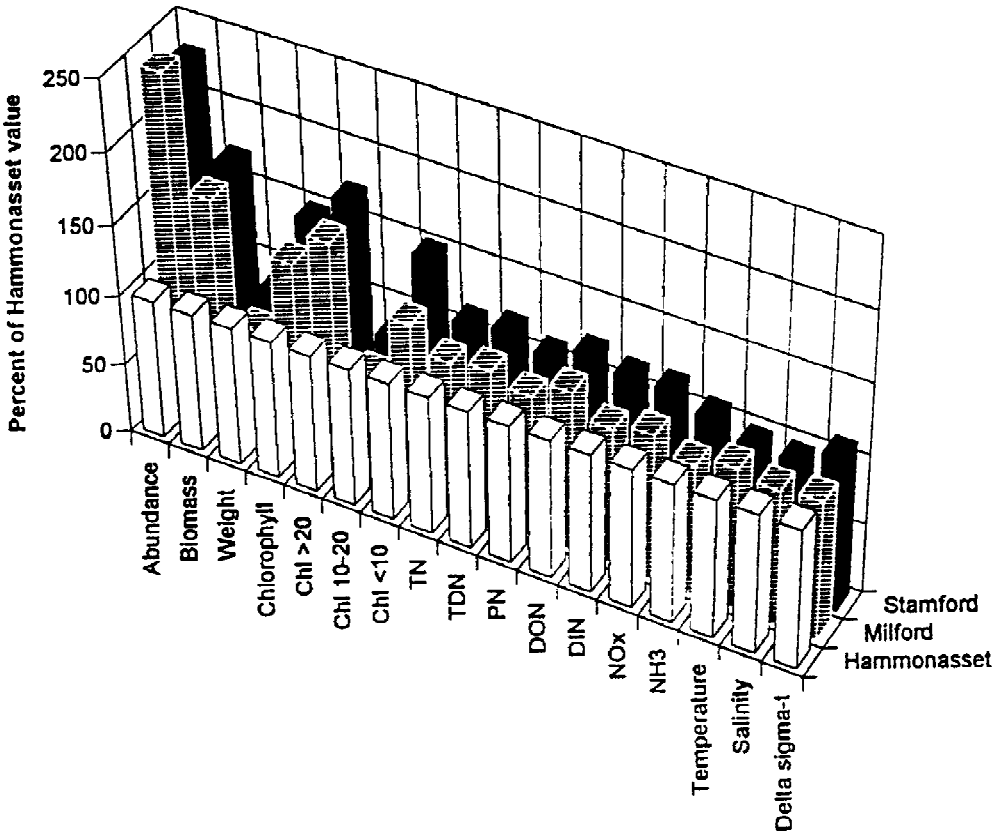


Figure 47. Trends among stations in copepod standing stock and individual weight, and trends among stations in chlorophyll concentrations, nitrogen concentrations and 3 water column physical properties.

best explained as a product of the east–west increase in the availability of large-sized phytoplankton. The summer–fall copepods, on the other hand, may have been limited by predation more than food, which may have led to their lesser abundance, and the greater uniformity of their east–west distribution.

Eutrophication can be thought of as a syndrome (suite of symptoms) that changes with the seasons. For example, the foremost symptom of eutrophication before a bloom might be abnormally high levels of dissolved nitrogen; whereas the symptoms during the bloom would become abnormally high chlorophyll concentrations and primary production maintained over an abnormally long period of time. After the bloom, there could be an abnormally high and persistent amount of herbivorous zooplankton biomass and production, and/or an increased amount of organic matter awaiting decomposition. Other symptoms of eutrophication include increased oxygen depletion below the summer thermocline (Welsh & Eller, 1991), and increased turbidity (Lund, 1969).

The eutrophication gradient, as indicated by the chlorophyll and nitrogen data, occurred primarily between Hammonasset and Milford. There was little difference between Milford and Stamford. This situation might reflect the fact that Milford is located about 5 k east of the mouth of the Housatonic river, the second largest river entering LIS, and a source of nitrogen. Therefore, the east–west gradient along the CT shore of LIS may be interrupted by this source. Hammonasset is located about 15 kilometers west of the mouth of the Connecticut River, which is the largest source of riverine freshwater to LIS. The plume of the CT river tends to the east, towards the nearby connection of LIS with the Atlantic Ocean (Fig. 1); moreover, Hammonasset is in a region where the net flow tends to be towards the east near-shore (O'Donnell, personal communication about drifter and current meter studies, and Welsh, personal communication about bathymetry and circulation in LIS). All of which suggests that nitrogen from the CT river might not as directly affect events at the Hammonasset station. Riley &

Conover (1956) suggested a mechanism whereby nutrients would be conserved and accumulated in LIS provided (1) residual circulation of water fits the classical estuarine pattern of up estuary (west) at the bottom, and down estuary (east) at the surface, (2) algal growth produces a vertical gradient of nutrients, and (3) a proportion of the algae produced at the surface is removed to deeper waters. Circulation in LIS appears to fit the classical estuarine circulation pattern in the eastern basin, but elsewhere it becomes more complex (Valle-Levinson & Wilson, 1984).

Nitrogen loading to LIS has more than doubled since colonial times, and about 50% of the nitrogen entering LIS comes from sewage treatment plants, which are clustered towards the western end (EPA, 1994; Welsh et al., 1995). Moreover, the East River, which connects western LIS to the waters surrounding New York City, is the single largest source of anthropogenic nitrogen. Increase in the sewage load may have leveled off since colonial times, but the form of the dissolved nitrogen fraction has shifted towards inorganic forms since the general conversion to secondary sewage treatment. The conversion is likely to have caused an increase in primary production because DIN is taken up directly by phytoplankton, whereas DON tends to require remineralization before usage. Increases in decomposition and biological oxygen demand below the thermocline are associated with increases in primary production, which may have caused an expansion of dangerously low oxygen levels in recent decades (Welsh et al., 1995). In short, the east–west gradient persists, and an increased inorganic nitrogen load contributes to the growth of phytoplankton, which might explain part of the difference between Riley & Conover's (1956) chlorophyll data and the data in this study.

The spatial variations in chlorophyll associated with eutrophication appear even larger than the seasonal variations if the western extremity of the sound (not sampled in this study) is included. Riley (1959) noted a 700% average increase in chlorophyll between the eastern and western extremes of LIS, reflecting a sharp upturn near the East River (New York City). Riley (1959) shows an increase an order of magnitude lower between the approximate longitudes of Hammonasset and Stamford, nearer the 50% estimate of this study. East to west increases in DIN are more subtle; they appear small or nonexistent in summer, but become more obvious after August (Riley & Conover, 1956). East to west increases in zooplankton did not seem to be clearly significant to Riley (1959) based on the data he had available. Since most of Riley's stations were further offshore than the stations used for this study, there is a chance that the significant east–west increase in copepods along the CT shore may not be typical of deep water areas in LIS.

Clearly, differences in prevailing conditions between inshore and offshore waters may affect the interpretation of these results as opposed to those of Riley and his group with respect to eutrophication and copepods in LIS as a whole. Increased concentrations of phytoplankton and zooplankton are noted by Riley (1955) in the shallow waters along the CT shore, thus eutrophication in LIS has a cross-Sound or south to north aspect as well as an east to west aspect. Hardy (1970) shows a distinct south to north increase of DIN concentrations in the central basin of LIS, which could be the root cause of the inshore-offshore gradients in phytoplankton and zooplankton Riley noted. Nearshore gradients in tidal mixing (Peterson, 1986), and influxes of fresh water (Riley, 1956) provide nutrients and alter the balance between stability and turbulence (Margalef, 1978; Schnitzer, 1979; Demers et al., 1986; Legendre & Lefévre, 1989). The general paradigm that small dinoflagellates replace large diatoms during the summer due to warmth, stratification, and low DIN is equivocal near shore, or any time there is a slight increase in NH_3 (Riley, 1969; Peterson, 1986). Inshore–offshore contrasts probably account for some of the difference between chlorophyll concentrations observed in this study, and those Riley (1959) shows at stations further offshore.

Processes considered

Broad generalities linking copepods and eutrophication are difficult to find because each system is different. In Osaka Bay and Tokyo Bay during summer, the median copepod weight decreased along a gradient of increasing eutrophication. Copepod biomass also decreased with eutrophication in Osaka Bay, but not in Tokyo Bay. Moreover, the species of copepods were shifted towards smaller varieties over the past several decades as eutrophication increased, and microphytoplankton gave way to picophytoplankton and nanophytoplankton (Uye, 1994). Why did Uye note reduced copepod biomass with eutrophication and we did not? Uye suggests, with good reason, that the displacement of large phytoplankton by small phytoplankton affected the copepods. In this study, copepod abundance, copepod biomass, and Chl >20 increased spatially with eutrophication. Thus it seems a paradox

that average copepod weight decreased with eutrophication in this study as well as Uye's. The copepods in LIS were 10–20% lighter at the stations with the most Chl >20, a finding for which we presently have no good explanation. Predators might be picking off more of the large copepods in the west than the east, and there is some evidence that larval fish may be more abundant at the western stations.

The next example is similar to what was observed in LIS, at least in the relation between copepods and phytoplankton. As water in the vicinity of the Southern Benguela upwelling aged and lost its charge of DIN, phytoplankton stocks decreased and dominance shifted from the size fraction >10 μm to the size fraction <10 μm. Moreover, copepods were fewer where phytoplankton <10 μm were dominant (Walker & Peterson, 1991; Painting et al., 1993). Copepod abundance and biomass gradients appear to occur where there are meaningful differences in productivity and cell size distribution. Extended flowerings appear more conducive to large populations of copepods than short blooms; moreover, the presence of a steady supply of food particles that are large enough seems to be a prerequisite. It would seem that some enrichment is required for large copepod populations, but that eutrophication beyond a certain point could be bad for them. Turbidity may become raised to such a level that the ability of flagellates to hold position in a narrowed euphotic zone allows them to displace the large phytoplankton that generally favor copepods. Perhaps the ratio of nitrogen – silicon becomes too high to allow diatoms to compete. Bottom water anoxia caused by eutrophication has also been implicated as a cause of change within the copepod community, with some species living associated with the benthos for parts of their life cycle (Purcell, 1994; Uye, 1994). The literature provides less detail on the seasonal behavior of DON than for DIN and PN, but the importance of DON as a bacterial substrate and source of recycled DIN is an accepted fact, and is supported by data from the larger study indicating large and consistent summer bacterial peaks. Our estimate that DON accounts for about 40% of TN in LIS on average is somewhat lower than the estimate (50–64%) of Sharp et al. (1982) for marine systems in general. Harris (1959) reported low DON values one spring, and there was similar evidence in this study, but neither one provided good evidence for a consistent yearly cycle. There were methodological problems and a single year record in the case of the Harris study, and in this one below average values extended from October right through spring in the second year. One might conjecture that the DON pool could be depleted by bacterial activity when phytoplankton production was limited by light because algae are such an important source of DON. Harris (1959) suggested the connection between DON and phytoplankton because DON increased in June along with a bloom of dinoflagellates. In the summer, or whenever DIN is depleted, DON becomes singularly important as a source for DIN regenerated by microbes. The present view emphasizes the importance of very rapid rates of nitrogen release and uptake in the water column, which produce a tight coupling between heterotrophic and autotrophic processes, while there is often virtually no detectable change in the pool of free dissolved nitrogen as a whole (Nixon & Pilson, 1983). We suspect that the higher DON observed in summer helps maintain primary production rates by increasing the rate of regeneration by the microbes.

The eastern station at Hammonasset had generally fewer copepods than has been observed in other sudies; however, stocks at Milford and Stamford were about as expected, except for unexpectedly small summer populations (Deevey, 1956; Peterson, 1986; Dam, 1989). Deevey's copepod abundance data are spatially averaged, and both Dam and Peterson worked west of Hammonasset, so the lower numbers of copepods at Hammonasset may not be unusual. Copepod biomass in the spring was dominated by *Temora longicornis*, and the peak biomass estimates for that species at Milford and Stamford were not significantly different from Dam's (1989). The species composition was in most ways indistinguishable from Peterson (1986) and Deevey (1956). However, both Deevey and Peterson found *Oithona* sp. more important during the summer and fall seasons than we did. The 202-μm net may not have retained many individuals of *Oithona* sp., based on the small narrow shape of the few individuals that did appear in our samples.

The typical lack of the summer copepod peaks that were seen by Deevey (1956) and Peterson (1986) suggests that the summer food-web may have changed somehow. Perhaps ctenophores are more abundant (our ctenophore debris observations would support this notion), or perhaps a shift has occurred away from copepods. However, it would be prudent to remember that there are inshore-offshore differences, and considerable year-to-year variability in LIS, before coming to any conclusions (although this study does represent a multi-year data set). The 202-μm net counts ranged from 183 to 59 542 ind m^{-3}, Deevey's (1956) 158-

μm net counts ranged from about 5000 to 150 000 ind m^{-3}, and her 363-μm net counts ranged from about 200 to 30 000 ind m^{-3}. A 158-μm mesh size retains more individuals than a 202-μm mesh, including small juveniles, whereas a 363-μm mesh retains fewer individuals than a 202-μm mesh. The fact that the counts were generally bracketed above and below by counts Deevey made with nets above and below in mesh size suggests that although changes may have occurred since 1956, they are not drastic changes.

Our 3 year larval fish work indicated that fish diversity was down as compared to S. Richard's and G. Riley's 1950s data. Overall, abundance was similar across our 3 east – west stations. When differences were encountered, they indicated higher levels at our western station. Also, over the course of 2 years of oxygen measurements at our 40-foot depth stations, hypoxic conditions were only encountered once. Given the above findings, larval fish should not experience food limitations nor severe oxygen stress, at least in near-shore waters. Thus, if juvenile and adult fish stocks are down, one must look elsewhere for a cause. Our species compositional work presented above (see results section on larval fish) indicates that two major factors may be overfishing and predation pressure (e.g., cormorants). If larval fish fail to capitalize on the high copepod biomass, ctenophores and other gelatinous zooplankton may be the beneficieries, i.e. we may be enhancing economically uninteresting gelatinous zooplankton at the expense of fish (Grieve-Parsons hypothesis, 1977). Indeed, anecdotal information and our ctenophore debris observations suggest that ctenophores are enhanced in the waters of the western Long Island Sound.

Conclusions and summary

Yearly and multi-year average concentrations of dissolved inorganic nutrient levels indicate similar (to only slightly higher in the west) nutrient concentrations across an east to west LIS gradient.

The relative proportioning among chemical species of nutrients often differs from west to east both contemporaneously as well as temporally, with NH_4 and DON at times more prevalent in the west (particularly in bottom waters).

The excess loading of nitrogen (and other nutrients) into the Sound appear to be converted to elevated biomass in the west (as evidenced by observed chlorophyll, phytoplankton and zooplankton concentration gradients).

Size-fractionated chlorophyll data indicate little east to west differences in the 10–20 μm size fraction while pointing to large differences in the <10 and >20 μm fractions which are both higher in the west.

Occurring along with the enhanced phytoplankton biomass is slightly enhanced bacterial densities and growth rates. The densities show interesting seasonal bacterial cycles and appear to be related not to total chlorophyll levels but to densities of the photosynthetic nanoplankton (PNANs).

Heterotrophic nanoplankton densities (HNANs) also are higher in the west and also appear to at times influence bacterial densities.

Species composition of phytoplankton routinely differ among west to east stations. These species compositional shifts appear to be related to N/P and N/Si ratios as well as to ratios among nitrogen chemical species.

Dissolved inorganic N/P ratios are routinely low among all stations with the west exhibiting lower levels than the east. However, total dissolved nitrogen /P ratios (which includes DON) are similar among stations and typically above the Redfield ratio of 16:1.

Associated with enhancement of bacterial, HNAN and <10 μm chlorophyll is significant enhancement of ciliate species diversity.

Microcrustacean (copepod) biomass also is extremely enhanced in the west vs. the east indicating that while stimulating the microbial loop, eutrophication is also enhancing secondary production preferred by larval fish, comb jellies and other jellyfish.

Copepod biomass as well as fecal pellet production likely is a significant contributor to hypoxia in Long Island Sound.

Our 3 year larval fish work indicated that fish diversity was down as compared to S. Richard's & G. Riley's 1950s data. Overall, abundance was similar across our 3 east to west stations. When differences were encountered, they indicated higher levels at our western station.

Over the course of 2 years of oxygen measurements, at our 40-foot depth stations, hypoxic conditions were only encountered one time. Given the above conditions larval fish should not experience food limitations nor severe O_2 stress, at least in near shore waters. Thus if juvenile and adult stocks are down one must look elsewhere for a cause.

If larval fish fail to capitalize on the high copepod biomass, ctenophore and other gelatinous zooplankton may be the beneficiaries, i.e. we may be enhancing economically uninteresting gelatinous zooplankton at

the expense of fish (Grieve-Parsons hypothesis). Indeed, anecdotal information suggests that ctenophores are enhanced in the waters of the western Long Island Sound.

Dual enhancement

Results from the completed study indicate that both the microbial loop as well as the copepod sector of the food web are enhanced west of Hammonasset. One implication of this 'dual enhancement' is that, in this instance, increased microbial activity does not take food away from the copepods. Since copepods are omnivorous, the increased numbers of protozoa may in fact have contributed to the increase in copepod standing stocks between Hammonasset and Milford.

New conventional wisdom

Excess nitrogen stimulates microbial loop and net phytoplankton biomass/production which in turn stimulates microcrustacean biomass/production, and fecal pellet release, which likely significantly fuel hypoxia, and whose ultimate fate is at this time unclear, but may very well be both gelatinous zooplankton as well as the sediments of Long Island Sound.

Acknowledgements

This research was made possible by a research grant to G.M. Capriulo and C. Yarish from the Long Island Sound Research Fund of the Connecticut Department of Environmental Protection. We wish to thank the following individuals and organizations for technical, intelectual and logistic support and contributions related to this project: Jack Schneider, Pete Marnane, Sally Richards (fish ID), Barbara Welsh, Patricia Day, Marcelo Morales, Kathy Beddows, Alex Shulgrin, Laura Donaldson, Helen Budrock, Fred Thurburg, Hans Dam, The Maritime Aquarium at Norwalk, CT, The National Marine Fisheries Service at Milford, CT, The Institute of Marine Sciences, University of Connecticut, Little Harbor Laboratories, Guilford, CT, The State University of New York at Purchase.

References

Agawin, N. S. R., C. M. Duarte & S. Agusti, 2000. Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. Limnol. Oceanogr. 45: 591–600.

Andersen, P. & H. M. Sørensen, 1986. Population dynamics and trophic coupling in pelagic microorganisms in eutrophic coastal waters. Mar. Ecol. Prog. Ser. 33:99–109.

Anderson, G. C., 1965. Fractionation of phytoplankton communities off the Washington and Oregon coasts. Limnol. Oceanogr. 10: 477–480.

Anderson, V. & P. Nival, 1989. Modeling of phytoplankton population dynamics in an enclosed water column. J. mar. biol. Ass. U.K. 69:625–646.

Anonymous, 1976–1983. Annual reports: monitoring the marine environment of Long Island Sound at Millstone nuclear power station. North East Utilities service co. Not published but may be photocopied on site.

Atlas, R. M. & R. Bartha, 1987. Microbial Ecology. Benjamin/Cummings Pub. Co. Inc.: 533 pp.

Azam, F., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil & F. Thingstad, 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. 10: 257–263.

Azam, F. & J. A. Fuhrman, 1984. Measurements of bacterioplankton growth in the sea and its regulation by environmental conditions. In Hobbie, J. & P. J. Williams (eds), Heterotrophic Activity in the Sea. Plenum Press. New York: 179–196.

Banse, K., 1992. Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. In Falkowski, P. G. & A. D. Woodhead (eds), Primary Productivity and Geochemical Cycles in the Sea. Plenum press, New York: 550 pp.

Bautista, B. & R. P. Harris, 1992. Copepod gut contents, ingestion rates and grazing impact on phytoplankton in relation to size structure of zooplankton and phytoplankton during a spring bloom. Mar. Ecol. Prog. Ser. 82: 41–50.

Bautista, B., R. P. Harris, P. R. G. Tranter & D. Harbour, 1992. *In Situ* copepod feeding and grazing rates during a spring bloom dominated by *Phaeocystis* sp. in the English Channel. J. Plankton Res. 14(5): 691–703.

Beeton, A. M., 1969. Changes in the environment and biota of the Great Lakes. In Eutrophication: Causes, consequences, correctives. Proceedings of a symposium, National Academy of Sciences: 150–187.

Berggreen, U., B. Hansen & T. Kiørboe, 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Mar. Biol. 99: 341–352.

Bidigare, R. R., 1991. Marine particles: analysis and characterization. In Hurd, D. C. & D. W. Spencer (eds), Geophysical Monograph 63. American Geophysical Union: 119–123.

Bird, D. F. & J. Kalff, 1986. Bacterial grazing by planktonic lake algae. Science 231: 493–494.

Bishop, J. W., 1967. Feeding rates of the ctenophore *Mnemiopsis leidyi*. Chesepeake Sci. 8:259–264.

Børsheim, K. Y., 1984. Clearance rates of bacteria-sized particles by freshwater ciliates, measured with non-disperse fluorescent latex beads. Oecologia, Berlin 63: 286–288.

Bøttger, R. & D. Schnack, 1986. On the effect of formaldehyde fixation on the dry weight of copepods. Meersforschung 31: 141–152.

Breteler, W. C. M & S. R. Gonzalez, 1988. Influence of temperature and food concentration on body size, weight and lipid content of two Calanoid copepod species. Hydrobiologia 167/168: 201–210.

Brown, C., W. J. Blogoslawski & L. P. Tettebach, 1988. Enumeration and identification of heterotrophic bacteria on oyster grounds of Long Island Sound. J. Shellfish Res. 7: 479–482.

Butler, M. & H. G. Dam, 1994. Production rates and characteristics of fecal pellets of the copepod *Acartia tonsa* under simulated bloom conditions: implications for vertical fluxes. Mar. Ecol. Prog. Ser. 114(1&2): 81–91.

Capriulo, G. M., 1990. Feeding related ecology of marine protozoa In Capriulo, G. M. (ed.), Ecology of Marine Protozoa. Oxford University Press, New York: 186– 259.

Capriulo, G. M. & E. G. Carpenter, 1980. Grazing by 35 – 202 μm microzooplankton in Long Island Sound. Mar. Biol. 56:319–326

Capriulo, G. M. & E. J. Carpenter, 1983. Abundance, species composition and feeding impact of tintinnid microzooplankton in central Long Island Sound. Mar. Ecol. Prog. Ser. 10: 277–288.

Capriulo, G. M. & D. V. Ninivaggi, 1982. A comparison of the feeding activities of field collected tintinnids and copepods fed with identical natural particle assemblages. Mar. Pel. Protozoa Microzoopl. Ecol. 58: 325–334.

Capriulo, G. M., R. A. Schnieder, & B. L. Dexter, 1988. Differential growth of *Euplotes vannus* fed fragmented *versus* unfragmented chains of *Skeletonema costatum*. Mar. Ecol. Prog. Ser. 47: 205–209.

Capriulo, G. M., E. B. Sherr & B. F. Sherr, 1991. Trophic behaviour and related community feeding activities of heterotrophic marine protists. In Reid, P. C. et al. (eds), Protozoa and their Role in Marine Procceses. NATO ASI series, Springer-Verlag: 219–265.

Capriulo, G.M., R. Troy, M. Morales, K. Beddows, H. Budrock, G. Wikfors and C. Yarish, 1993. Possible eutrophication-related enhancement of the microbial loop in Long Island Sound and consequences for shellfish. J. of Shellfish Research 12(1): 107.

Capriulo, G.M., 1997. Mechanisms of hypoxia development and future research needs, Long Island Sound Conference Panel Session Summary. Proceedings of the 3rd Long Island Sound Research Conference. Connecticut Sea Grant Publication CTSG-97-08, pp 86–88.

Caron, D. A. & J. Goldman, 1990. Protozoan nutrient regeneration. In Capriulo, G. M. (ed.), The Ecology of Marine Protozoa. Oxford University Press, N.Y.: 283–306.

Carpenter, S. R., J. F. Kitchell, & J. R. Hodgson, 1985. Cascading trophic interactions and lake productivity: fish predation and herbivory can regulate lake ecosystems. Bioscience 35(10): 634–639.

Conover, R. J., 1956. Biology of *Acartia tonsa* and *Acartia clausi*. In Oceanography of Long Island Sound. Bulletin of the Bingham Oceanographic Collection. Peabody Museum of Natural History, Yale University. 15: 156–233.

Conover R. J., 1978. Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11: 338–345.

Conover, R. J. & M. E. Huntley, 1980. General rules of grazing in pelagic ecosystems. In Falkowski, P. (ed.), Primary Production in the Sea. Plenum Press, New York: 461–485.

Cowles, T. J., R. J. Olson & S. W. Chisholm, 1988. Food selection by copepods: discrimination on the basis of food quality. Mar. Biol. 100: 41–49.

Cushing, D. H., 1975. Marine Ecology and Fisheries. Cambridge Univ. Press: 278 pp.

Dam, H. G., 1989. The dynamics of copepod grazing in Long Island Sound. Doctoral dissertation. State Univ. of New York.

Dam, H. G. & W. T. Peterson, 1988. The effect of temperature on the gut clearance rate constant of planktonic copepods. J. exp. mar. Biol. Ecol. 123: 1–14.

Dam, H. G. & W. T. Peterson, 1991. *In situ* feeding behavior of the copepod *Temora longicornis*: effects of seasonal changes in chlorophyll size fractions and female size. Mar. Ecol. Prog. Ser. 71: 113–123.

Dam, H. G., W. T. Peterson & D. C. Bellantoni, 1994. Seasonal feeding and fecundity of the calanoid copepod *Acartia tonsa* in Long Island Sound: is omnivory important to egg production? In Ferrari, F. D. & B. P. Bradley (eds), Ecology and Morphology of Copepods. Hydrobiologia 292/293: 191–199.

Deevey, G. B., 1956. Zooplankton. In Oceanography of Long Island Sound. Bulletin of the Bingham Oceanographic Collection. Peabody Museum of Natural History, Yale University. 15: 113–155.

de Jonge, V. N., W. Boynton, C. F. D'Elia, R. Elmgren & B. L. Welsh, 1995. Responses to developements in eutrophication in four different North Atlantic estuarine systems. In Dyer, K. R. & R. J. Orth (eds), Changes in Fluxes in Estuaries. Olsen & Olsen International Symposium Series: 179–195.

Demers, S., L. Legendre & J. C. Therriault, 1986. Phytoplankton responses to vertical mixing. In Bowman, J., M. Yentsch & W. T. Peterson (eds), Lecture Notes on Coastal and Estuarine Studies, Vol. 17. Tidal Mixing and Plankton Dynamics. Springer-Verlag, Berlin, Heidelberg.

Dolan, J. R., 1991. Microphagous ciliates in mesohaline Chesepeake Bay waters: estimates of growth rates and consumption by copepods. Mar. Biol. 111: 303–309.

Dorsey, T. E., W. McDonald & O. A. Roels, 1977. A heated biuret-Folin protien assay which gives equal absorbence with different proteins. Anal. Biochem 78: 156–164.

Dorsey, T. E., W. McDonald & O. A. Roels, 1978. Measurements of phytoplankton protein content with the heated biuret-Folinassay. J. Phycol. 14: 167–171.

Ducklow, H. W., 1983. Production and fate of bacteria in the sea. Bioscience 33(8): 494–499.

Durbin, E. G. & A. G. Durbin, 1978. Length and wieght relationships of *Acartia clausi* from Narragansett Bay, Rhode Island. Limnol. Oceanogr. 23: 958–969.

Durbin et al., 1992. Body size and egg production in the marine copepod *Acartia hudsonica* during a winter–spring bloom in Narragansett Bay. Limnol. Oceanogr. 37(2): 342–360.

Egge, J. K. & D. L. Aksnes, 1992. Silicate as regulating nutrient in phytoplankton competition. Mar. Ecol. Progr. Ser. 83: 281–299.

EPA, 1994. The Long Island Sound Study: The Comprehensive Conservation and Management Plan. EPA Publication of the Long Island Sound Study. Long Island Sound Office of the U.S. Environmental Protection Agency, State University of New York at Stony Brook, New York: 168 pp.

Fenchel, T., 1967. The ecology of marine microbenthos. The quantitative importance of ciliates as compared with metazoans in various types of sediment. Ophelia 4: 121–137.

Fenchel, T., 1968. The ecology of marine microbenthos. 2. The food of marine benthic ciliates. Ophelia 5: 73–121.

Fenchel, T., 1982. Ecology of heterotrophic microflagellates. 4: Quantitative occurrence and importance of bacterial consumers. Mar. Ecol. Prog. Ser. 9: 35–42.

Fenchel, T. & B. J. Finlay, 1983. Respiration rates in heterotrophic, free-living protozoa. Microb. Ecol. 9: 99–122.

Fenchel, T., L. D. Kristensen & L. Rasmussen, 1990. Water column anoxia: vertical zonation of planktonic protozoa. Mar. Ecol. Prog. Ser. 62: 1–10.

Fisher, R. A., 1950. The significance of deviations from expectation in a Poisson series. Biometrics. 1: 17–24.

Frost, B. W., 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17(6): 805–815.

Fuhram, J. A., J. W. Ammerman & F. Azam, 1980. Bacterioplankton in the coastal euphotic zone: distribution, activity and possible relationships with phytoplankton. Mar. Biol. 60: 201–207.

Fuhram, J. A. & F. Azam, 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: Evaluation of field results. Mar. Biol. 66: 109–120.

Furnas, M. J., 1990. *In situ* growth rates of marine phytoplankton: approaches to measurement, community and species growth rates. J. Plankton Res. 12: 1117–1151.

Gast, V., 1985. Bacteria as a food source for microzooplankton in the Schlei Fjord and Baltic Sea with special reference to ciliates. Mar. Ecol. Prog. Ser. 22: 107–120.

Geider, R. J., T. Platt & J. A. Raven, 1986. Size dependence of growth and photosynthesis in diatoms: a synthesis. Mar. Ecol. Prog. Ser. 30: 93–104.

Gifford, D. J. & M. J. Dagg, 1988. Feeding of the estuarine copepod *Acartia tonsa*: Carnivory vs.herbivory in natural microplankto assemblages. In Paffenhoefer, G. A. & H. J. Price (eds), Zooplankton Behavior Symposium, Savannah, GA (U.S.A.), 13–16 Apr 1987. Bull. mar. Sci. 43(3): 458–468.

Glibert, P. M., C. A. Miller, C. Garside, M. R. Roman & G. B. McManus, 1992. NH_4^+ regeneration and grazing: interdependent processes in size fractionated $^{15}NH_4^+$ experiments. Mar. Ecol. Prog. Ser. 82: 65–74.

Goldman, J. C., D. A. Caron, O. K. Andersen & M. R. Dennett, 1985. Nutrient cycling in a microflagellate food chaIn 1. Nitrogen dynamics. Mar. Ecol. Prog. Ser. 24: 231–242.

Greve, W. & T. R. Parsons, 1977. Photosynthesis and fish production: hypothetical effects of climate change and pollution. Helgolander wiss. Meeresunters. 30: 666–672.

Haas, L. W. & K. L. Webb, 1979. Nutritional mode of several non-pigmented micro-flagellates from the York River estuary, Virginia. J. exp. mar. Biol. Ecol. 39: 125–134.

Hagstrøm, A., 1984. Aquatic bacteria: measurements and significance of growth. In Klug, M. J. & C. A. Reddy (eds), Current Perspectives in Microbiology. American Society for Microbiology, Washington, D.C.: 495–501.

Hagstrøm, A., U. Larsson, P. Horstedt & S. Norwalk, 1979. Frequency of dividing cells, a new approach to the determination of bacterial growth rates in aquatic environments. Appl. Env. Microbiol. 37: 805–812.

Hansen, F. C., M. Reckermann, W. C. M. Klein Breteler & R. Riegman, 1993. *Phaeocystis* blooming enhanced by copepod predation on protozoa: evidence from incubation experiments. Mar. Ecol. Prog. Ser. 102: 51–57.

Hardy, C. D., 1970. Hydrographic data report: Long Island Sound – 1969. Technical Report No. 4. Marine Sciences Research Center. State University of New York. Stony Brook, NY. 130 pp.

Harris, E., 1959. The nitrogen cycle in Long Island Sound. Bulletin of the Bingham Oceanographic Collection. Peabody Museum of Natural History. Yale Univ. 17: 31–65.

Harris, E. & G. A. Riley, 1956. Chemical composition of the plankton. In Oceanography of Long Island Sound. Bull. Bingham Oceanogr. Collection, Peabody Museum of Natural History, Yale University 15: 315–323.

Harris, G. P., 1986. Phytoplankton Ecology – Structure, Function and Fluctuation. Chapman and Hall, N.Y.

Harrison, P. J., D. H. Turpin, P. K. Bienfang & C. O. Davis, 1986. Sinking as a factor affecting phytoplankton species succession: the use of selective loss, semi-continuous cultures. J. exp. mar. Biol. Ecol. 99: 19–30.

Hobbie, J. E., R. J. Daley & S. Jasper, 1977. Use of nuclepore filters for counting bacteria by fluorescence microscopy. Appl. Envir. Microbiol. 33: 1225–1228.

Hoch, M. P. & D. L. Kirchman, 1993. Seasonal and inter-annual variability in bacterial production and biomass in a temperate estuary. Mar. Ecol. Prog. Ser. 98: 283–295.

Howarth, R. W. & J. J. Cole, 1985. Molybdenum availability, nitrogen limitation, and phytoplankton growth in natural waters. Science 229: 653–655.

Hulburt, E. M.,1988. Diversity, equilibrium and adaptation as related by equivalence in the oceanic phytoplankton. Biol. Oceanogr. 6: 1–21.

Hunter, M. S. & P. W. Price, 1992. Playing chutes and ladders: heterogeniety and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73(3): 724–732.

Huntley, M. & C. Boyd, 1984. Food limited growth of marine zooplankton. Am. Nat. 124(4): 455–478.

Ikeda, T., 1974. Nutritional ecology of marine zooplankton. Mem. fac. fish. Hokkaido univ. 22: 1–97.

Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Mar. Biol. 85: 1–11.

Johannes, R. E., 1964. Phosphorus excretion and body size in marine animals: microzooplankton and nutrient regeneration. Science 146: 923–924.

Johannes, R. E., 1965. Influence of marine protozoa on nutrient regeneration. Limnol. Oceanogr. 10: 434–442.

Johnson, J. M., 1993. The recycling of inorganic nutrients in the upper water column during seasonal stratification in western Long Island Sound. M.S. thesis, Univ. CT.

Johnson, P. W. & J. McN. Sieburth, 1979. Chroococcoid cyanobacteria in the sea: a ubiquitous and diverse phototrophic biomass. Limnol. Oceanogr. 24: 928–935.

Johnson, P. W. & J. McN. Sieburth, 1982. *In situ* morphology and occurrence of eucaryotic phototrophs of bacterial size in the picoplankton of estuarine and oceanic waters. J. Phycol. 18: 318–327.

Johnson, T. D., 1987. Growth and regulation of the population of *Parvocalanus crassirostris* (Copepoda: Calanoida) in Long Island Sound, New York. Doctoral dissertation, State University of New York at Stony Brook.

Jones, R., 1976. Growth of fishes. In Cushing, D. H. & J. J. Walsh (eds), Ecology of the Seas. Blackwell Scientific, Oxford: 251–279.

Jumars, P. A., D. L. Penry, J. A. Baross, M. J. Perry & B. W. Frost, 1989. Closing the microbial loop: dissolve carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep Sea Res. 36(4):483–495.

Ketchum, B. H., 1969. Eutrophication of estuaries. In Eutrophication: Causes, consequences, correctives. Proceedings of a symposium, National Academy of Sciences: 197–209.

Kiørboe, T., 1989. Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in a herbivorous copepod. Mar. Ecol. Prog. Ser. 55: 229–234.

Kiørboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. In Baxter, J. H. S. & A. J. Southward (eds), Advances in Marine Biology. Academic Press (29): 2–61.

Kiørboe, T., P. Munk, K. Richardson, V. Christensen & H. Paulsen, 1988. Plankton dynamics and larval herring growth, drift, and survival in a frontal area. Mar. Ecol. Prog. Ser. 44: 205–219.

Kiørboe, T., F. Mohlenberg, & K. Hamburger, 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and compostion of specific dynamic action. Mar. Ecol. Prog. Ser. 26: 85–97.

Kiørboe, T. & T. G. Nielsen, 1994. Regulation of zooplankton biomass and production in a temperate coastal ecosystem. 1. Copepods. Limnol. Oceanogr. 39(3): 493–507.

Kirchman, D. L., H. W. Ducklow & R. Mitchell, 1982. Estimates of bacterial growth from changes in uptake rate and biomass. Appl. Envir. Microbiol. 44: 1296–1307.

Klein-Breteler, W. C. & S. R. Gonzalez, 1988. Influence of temperature and food concentration on body size, and lipid content of two calanoid copepod species. Hydrobiologia 167/168: 201–210.

Kremer, P., 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansset Bay, Rhode Island. Estuaries 2:97–105.

Larsson, U. & A. Hagstrøm, 1982. Fractionated phytoplankton primary production, exudate release, and bacterial production in a Baltic eutrophication gradient. Mar. Biol. 67: 57–70.

Lasker, R. (ed.), 1981. Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries. Washington Sea Grant Program, Univ. of Washington Press, Seattle: 131 pp.

Lee, J. J., E. B. Small, D. H. Lynn & E.C. Bovee, 1985. Some techniques for collecting, cultivating and observing protozoa. In Lee, J. J., S. H. Hunter & E. C. Bovee (eds), An Illustrated Guide to the Protozoa. Allen Press, Lawrence, Kansas: 629 pp.

Legendre, L. & J. Le Févre, 1989. Hydrodynamical singularities as controls of recycled *versus* export production in oceans. In Berger, W. H. V. S. Smetacek & G. Wefer (eds), Productivity of the Ocean: Present and Past. John Wiley and Sons Limited: 49–63.

Lessard, E. J. & E. Swift, 1985. Species specific grazing rates of heterotrophic dinoflagellates in oceanic waters, measured with a dual-label radioisotope technique. Mar. Biol. 87: 289–296.

Lignell, R., A. S. Heiskanen, H. Kuosa, K. Gundersen, P. Kuuppo-Leinikki, R. Pajuniemi, A. Uitto, 1993. Fate of a phytoplankton spring bloom in the planktonic food web in the northern Baltic. Mar. Ecol. Prog. Ser. 94: 239–252.

Long Island Sound Study Annual Report, 1988. U.S. Environmental Protection Agency, Region 2. U.S. Government Printing Office: 36 pp.

Long Island Sound Study Annual Report, 1989/1990. U.S. Environmental Protection Agency, Region 2. U.S. Government Printing Office: 37 pp.

Long Island Sound Study Annual Report, and Interim Actions for Hypoxia Management, 1990. U.S. Environmental Protection Agency, Region 2. U.S. Government Printing Office.

Longhurst, A. R., A. W. Bedo, W. G. Harrison, E. J. Head & D. D. Sameto, 1990. Verical flux of respiratory carbon by diel migrant biota. Deep Sea Res. 37: 685–694.

Loyd, M., 1967. 'Mean Crowding'. J. anim. Ecol. 36: 1–30.

Lund, J. W. G., 1969. Phytoplankton. In Eutrophication: Causes, Consequences, Correctives. Proceedings of a Symposium, National Academy of Sciences: 306–330.

Lutz, P. E., 1986. Invertebrate zoology. Addison Wesley: 734 pp.

Malone, T. C., 1971. The relative importance of nanoplankton and netplankton as primary producers in tropical oceanic and neritic phytoplankton communities. Limnol. Oceanogr. 16: 633–639.

Malvin, G. M. & S. C. Wood, 1992. Behavioral hypothermia and survival of hypoxic protozoans *Paramecium caudatum*. Science 255: 1423–1425.

Mann, K. H., 1982. Ecology of Coastal Waters: A Systems Approach. University of California Press: 321 pp.

Mann, K. H. & J. R. N. Lazier, 1991. Dynamics of Marine Ecosystems. Blackwell Scientific Publications: 475 pp.

Mantoura, R. F., B. Li, W. Gieskes, H. Maske & R. Bidigare, 1990. In Core Measurements Protocols, report no. 6, chapter 9: 17–19.

Margalef, R., 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta 1(4): 493–509.

McManus, G. B. & J. A. Fuhrman, 1986. Bacterivory in seawater studied with the use of inert fluorescent particles. Limnol. Oceanogr. 31: 420–426.

McManus, G. B. & J. A. Fuhrman, 1988. Clearance of bacteria sized particles by natural populations of nanoplankton in the Chesapeake bay outflow plume. Mar. Ecol. Prog. Ser. 42:199–206.

McQueen, D. J., M. R. S Johannes, J. R. Post, T. J. Stewart & D. R. S. Lean, 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59(3): 289–309.

Montagnes, D. J. S., D. H. Lynn, J. C. Raff & W. D. Taylor, 1988. The annual cycle of heterotrophic planktonic ciliates in the waters surrounding the Isles of Shoales, Gulf of Maine: an assessment of their trophic role. Mar. Biol. 99: 21–30.

Monteleone, D. M., W. T. Peterson & G. C. Williams, 1987. Interannual variations in density of sand lance, *Ammodytes americanus,* larvae in Long Island Sound, 1951–1983. Estuaries, 10: 246–254.

Morris, I. And H. Glover, 1981. Physiology of photosynthesis by marine coccoid cyanobacteria – some ecological implications. Limnol. Oceanogr. 26: 957–961.

Mullin, M. M., 1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. Limnol. Oceanogr. 17: 805–815.

Murdoch, W. W., R. M. Nisbet, E. McCauly, A. M. DeRoos & W. S. C. Gurney, 1998. Plankton abundance and dynamics across nutrient levels: test of hypothesis. Ecology, 79: 1339–1356.

Ng, S. J., M. I. Lucas, W. T. Peterson, P. C. Brown, L. Hutchings, & B. A. Mitchell-Innes, 1993. Dynamics of bacterioplankton, phytoplankton and mesozooplankton communities during the develpment of an upwelling plume in the southern Benguela. Mar. Ecol. Prog. Ser. 100: 35–53.

Nielsen, T. G., B. Lokkegaard, K. Richardson, F. B. Petersen & L. Hansen, 1993. Structure of plankton communities in the Dogger Bank area (North Sea) during a stratified situation. Mar. Ecol. Prog. Ser. 95: 115–131.

Nixon, W. S. & M. Q. Pilson, 1983. Nitrogen in Estuarine and coastal ecosystems. In Nitrogen in the marine environment. Academic Press Inc.: 565–648.

O'Connors, H. B., L. F. Small, & P. L. Donaghay, 1976. Particle size modification by two size classes of the estuarine copepod *Acartia clausi*. Limnol. Oceanogr. 21: 300–308.

O'Connors, H. B., D. C. Biggs, & D. V. Ninivaggi, 1980. Particle-size-dependent maximum grazing rates for *Temora longicornis* fed natural particle assemblages. Mar. Biol. 56:65–70.

O'Connors, H. B., C. F. Wurster, C. D. Powers & R. G. Rowland, 1978. Polychlorinated biphenyls may alter marine trophic pathways by reducing phytoplankton size and production. Science 201: 737–739.

Olson, R. L., 1975. Masters Thesis, State Univ. of New York at Stony Brook, N. Y.

Omori, M. & T. Ikeda, 1984. Methods in Marine Zooplankton Ecology. John Wiley & Sons. 332 pp.

Painting, S. J., M. I. Lucas, W. T. Peterson, P. C. Brown, L. Hutchings & B. A. Mitchell-Innes, 1993. Dynamics of bacterioplankton, phytoplankton, and mesoplankton communities during the development of an upwelling plume in the southern Benguela. Mar. Ecol. Prog. Ser. 100: 35–53.

Parsons, T. R., Y. Maita & C. M. Lalli, 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, Oxford: 173 pp.

Pechenick, J. A., 1985. Biology of Invertebrates. Prindle, Weber, and Schmidt: 513 pp.

Peduzzi, G. J., 1992. Zooplankton activity fueling the microbial loop: differential growth response of bacteria from oligotrophic and eutrophic waters. Limnol. Oceanogr. 37(5): 1087–1092.

Peterson, W. T., 1985. Abundance, age structure and *in situ* egg production rates of the copepod *Temora longicornis* in Long Island Sound, New York. Bull. mar. Sci. 37: 726–738.

Peterson, W. T., 1986. The effects of seasonal variation in stratification on plankton dynamics in Long Island Sound. In Bowman, J., M. Yentch & W. T. Peterson (eds), Lecture Notes on Coastal and Estuarine Studies, Vol. 17, Tidal Mixing and Plankton Dynamics. Springer-Verlag: 297–320.

Peterson, W. T. & D. C. Bellantoni, 1987. Relationships between water column stratification, phytoplankton cell size and copepod fecundity in Long Island Sound and off central Chile. S. Afr. J. mar. Sci. 5: 411–421.

Peterson, W. T., L. Hutchings, J. A. Hugget & J. L. Largier, 1992. Anchovy spawning in relation to the biomass and the replenishment rate of their copepod prey on the Western Agulhas Bank. In Payne, A. I. L., K. H. Mann, K. H. Brink & R. Hillborn (eds), Benguela Trophic Functioning. South African J. mar. Sci. 12: 487–500.

Pomeroy, L. R., 1974. Significance of microorganisms in carbon and energy flow in marine ecosystems. In Klug, M. J. & C. A. Reddy (eds), Current Perspectives in Microbial Ecology. Amer. Soc. Microbiol., Washington, D. C.: 405 pp.

Power, M. E., 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73(3) 733–746.

Price, H. J., G. A. Paffenhoefer & J. R. Strickler, 1983. Modes of cell capture in calanoid copepods. Limnol. Oceanogr. 28(1): 116–123.

Price, H. J. & G. A. Paffenhoefer, 1984. Effects of feeding experience in the copepod *Eucalanus pileatus*: A cinematographic study. Mar. Biol. 84(1): 35–40.

Proctor, L. M. & J. A. Fuhram, 1990. Viral mortality of marine bacteria and cyanobacteria. Nature, 343: 60–62.

Purcell, J. E., J. R. White & M. R. Roman, 1994. Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesepeake Bay. Limnol. Oceanogr. 39(2): 263–278.

Redfield, A. C., 1934. On the proportion of organic derivatives in sea water and their relation to the composition of plankton. James Johnston Memorial Volume. Univ. Press of Liverpool: 176–192.

Riley, G. A., 1955. Review of the oceanography of Long Island Sound. In Papers in Marine biology and oceanography Pergamaon Press Ltd., London: 224–238.

Riley, G. A., 1956a. Physical oceanography. In Oceanography of Long Island Sound. Bulletin of the Bingham Oceanographic collection. Peabody Museum of Natural History, Yale University. 15: 15–46.

Riley, G. A., 1956b. Production and utilization of organic matter. In Oceanography of Long Island Sound. Bulletin of the Bingham Oceanographic Collection. Peabody Museum of Natural History, Yale University 15: 324–343.

Riley, G. A., 1959. Oceanography of Long Island Sound, 1954–1955. In Oceanography of Long Island Sound and Guide for Preparing Figures. Bulletin of the Bingham Oceanographic Collection. Peabody Museum of Natural History, Yale University 17: 9–29.

Riley, G. A., 1969. The plankton of estuaries. In Lauff, G. (ed.), Estuaries. A.A.A.S. publication no. 83: 757 pp.

Riley, G. A., S. Conover, G. Deevey, R. Conover, S. B. Wheatland, E. Harris & H. L. Sanders, 1956. Oceanography of Long Island Sound 1952–1954. Bulletin of the Bingham Oceanographic Collection. V. 15. Peabody Museum of Natural History, Yale University: 414 pp.

Riley, G. A., E. Harris, H. M. Schurr, P. J. Wangersky, S. W. Richards & R. W. Covill, 1959. Oceanography of Long Island Sound and Guide for Preparing Figures. Bulletin of the Bingham Oceanographic Collection. V. 17. Peabody Museum of Natural History, Yale University: 153 pp.

Riley, G. A. & S. M. Conover, 1956. Chemical Oceanography. In Oceanography of Long Island Sound. Bulletin of the Bingham Oceanographic Collection. Peabody Museum of Natural History, Yale University 15: 47–61.

Riley, G. A. & S. M. Conover, 1967. Phtytoplankton of Long Island Sound 1954–1955. Bulletin of the Bingham Oceanographic Collection. Peabody Museum of Natural History, Yale University 19:5–33.

Rohlich, G. A., 1969. Introduction, summary, and recommendations. In Eutrophication: Causes, consequences, Correctives. Proceedings of a symposium. National Academy of Sciences: 661 pp.

Rose, M., 1933. Faune de France 26, copepods pelagiques. Federation Francaise des Societes de Sciences Naturelles: 374 pp.

Ryther, J. H. & W. M. Dunstan, 1971. Nitrogen, Phosphorus, and eutrophication in the coastal marine environment. Science 13: 1008–1013.

Sakshaug, E., K. Andersen, S. Myklestad & S. Olsen, 1983. Nutrient status of phtoplankton communities in Norwegian waters (marine, brackish and fresh) as revealed by their chemical composition. J. Plankon Res. 5: 175–196.

Sakshaug, E. & Y. Olsen, 1986. Nutrient status of phytoplankton blooms in Norwegian waters and algal strategies for nutrient competition. Can. J. Fish. aquat. Sci. 43: 389–396.

Sanders, J. G., S. J. Cibik, C. F. D'Elia & W. R. Boynton, 1987. Nutrient enrichment studies in a coastal plain estuary: changes in phytoplankton species composition. Can. J. Fish. aquat. Sci. 44: 83–90.

Sanders, R. W. & K. G. Porter, 1988. Phagotrophic phytoflagellates. In Marshall, K. C. (ed.), Advances in Microbial Ecology. V. 10. Plenum Pub. Corp.

Sanders, R. W., D. A. Caron & V.-G. Berninger, 1992. Relationships between bacteria and heterotrophic nanoplankton in marine and fresh waters: an inter-ecosystem comparison. Mar. Ecol. Prog. Ser. 86: 1–14.

Sars, G. O., 1903. An Account of the Crustacea of Norway, Vol. IV, *Copepoda calanoida*. Bergen Museum: 169 pp.

Schnitzer, M. B., 1979. Vertical stability and the distribution of phytoplankton in Long Island Sound. Masters thesis, SUNY, Stoney Brook.

Sharp, J. H., A. C. Frake & G. B. Hillier, 1982. Modeling nutrient regeneration in the open ocean with an aquarium system. Mar. Ecol. Prog. Ser. 8: 15–23.

Sherr, E. B. & B. F. Sherr, 1987. High rates of consumption of bacteria by pelagic ciliates. Nature 325: 710–711.

Sherr, E. & B. F. Sherr, 1988. Role of microbes in pelagic food webs: A revised concept. Limnol. Oceanogr. 33(5): 1225–1227.

Sherr, E. B., B. F. Sherr & G. A. Paffenhofer, 1986. Phagotrophic protozoa as food for metazoans: a 'missing' trophic link in marine pelagic food webs. Mar. Microbial food webs 1: 61–80.

Sherr, E. B., D. A. Caron & B. F. Sherr, 1994. Staining of heterotrophic protists for visualization via epifluorescence microscopy. In Kemp, P. F., B. F. Sherr, E. B. Sherr & J. J. Cole (eds), Handbook of Methods in Aquatic Microbial Ecology. Lewis Publishers, Boca Raton, FL., U.S.A.: 213–228.

Smetacek, V. S., 1981. The annual cycle of protozooplankton in the Kiel Bight. Mar. Biol. 63: 1–11.

Snedecor, G. W. & G. Cochran, 1967. Statistical Methods. The Iowa State Univ. Press: 593 pp.

Søndergaard, M., L. M. Jensen & G. Aertebjerg, 1991. Picoalgae in Danish coastal waters during summer stratification. Mar. Ecol. Prog. Ser. 79: 139–149.

Strickland, J. D. H. & T. R. Parsons, 1972. A Practical Handbook of Seawater Analysis. Fisheries Res. Board of Canada: 310 pp.

Strickland, J. D. H. & T. R. Parsons, 1977. A Practical Handbook of Seawater Analysis. Bull. Fish. Res. Bd Can. 167: 1–310.

Strong, D. R., 1992. Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. Ecology 73(3): 747–754.

Tettelbach, S. T., L. M. Petti & W. J. Blogoslawski, 1984. Survey of *Vibrio* associated with a New Haven Harbor Shellfish bed, emphasizing recovery of larval oyster pathogens. In Colwell, R. R. (ed.), Vibrios in the Environment. John Wiley and Sons, New York.

Thigstad, T. F. & F. Rassoulzadegan, 1999. Conceptual models for the biogeochemical role of the photic zone microbial food web, with particular reference to the Mediterranean Sea. Prog. Oceanogr. 44: 271–286.

Thomas, W. H. & D. L. R. Seibert, 1977. Effects of cooper on the dominance and diversity of algae: controlled ecosystem pollution experiment. Bull. mar. Sci. 27: 23–33.

Tilman, D., S. S. Kilham & P. Kilham, 1982. Phytoplankton Community Ecology: The Role of Limiting Nutrients. Ann. Rev. Ecol. Syst. 13: 349–372.

Tilman, D., R. Kiesling, R. Sterner, S. S. Kilham & F. A. Johnson, 1986. Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch. Hydrobiol. 106: 473–485.

Todd, C. D. & M. S. Laverick, 1991. Coastal Marine Zooplankton: a Practical Manual for Students. Cambridge Univ. Press: 106 pp.

UNESCO, 1968. Zooplankton sampling: monographs on oceanographic methodology, 2. United Nations Educational, Scientific, and Cultural Organization Press, Paris, France: 174 pp.

Uye, S., 1994. Replacement of large copepods by small ones with eutrophication of embayments: causes and consequences. Hydrobiologia 292/293: 513–519.

Uye, S. & N. Shibuno, 1992. Reproductive biology of the planktonic copepod *Paracalanus* sp. in the Inland Sea of Japan. J. Plankton Res. 14(3): 343–358.

Valle-Levinson, A. & R. A. Wilson, 1984. Effects of sill processes and tidal forcing on exchange in eastern Long Island Sound. J. Geophysical Res. 99: 12 667–12 681.

Valliela, I., 1984. Marine Ecological Procceses. Springer-Verlag: 546 pp.

Vanderploeg, H. A., 1990. Feeding mechanisms and particle selection in suspension feeding zooplankton. In Wotton, R. S. (ed.), The Biology of Particles in Aquatic Systems. CRC Press.

Van Donk, E. & S. S. Kilham, 1990. Temperature effects on silicon- and phosphorus-limited growth and competitive interactions among three diatoms. J. Phycol. 26: 40–50.

Verheye, H. M., L. Hutchings, J. A. Huggets & S. J. Painting, 1992. Mesoplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. In Payne, A. I. L., K. H. Mann, K. H. Brink & R. Hillborn (eds), Benguela Trophic Functioning. South African J. mar. Sci. 12: 561–584.

Walker, D. R. & W. T. Peterson, 1991. Relationships between hydrography, phytoplankton production, biomass, cell size and species composition, and copepod production in the southern Benguela upwelling system in April 1988. S. Afr. J. mar. Sci. 11: 289–305.

Welsh, B. L., 1992. Phsical oceanography of Long Island Sound: an ecological perspective. Univ. of Connecticut plenary paper from Long Island Sound scientific conference Oct. 23–24, 1992, proceedings, Connecticut Sea Grant Publication.

Welsh, B. L., R. I. Welsh & M. L. Digiacomo-Cohen, 1995. Quantifying hypoxia and anoxia in Long Island Sound. In Dyer, K. R. & R. J. Orth (eds), Changes in Fluxes in Estuaries. Olsen & Olsen International Symposium Series: 131–137.

Welsh, B. L. & F. C. Eller, 1991. Mechanisms controlling summertime oxygen depletion in western Long Island Sound. Estuaries 14:265–278.

Wheeler, P. A. & D. L. Kirchman, 1986. Utilization of inorganic and organic nitrogen by bacteria in marine systems. Limnol. Oceanogr. 31(5): 998–1009.

White, J. R. & M. R. Roman, 1992. Egg production by the calanoid copepod *Acartia tonsa* in the mesohaline Chesapeake Bay: the importance of food resources and temperature. Mar. Ecol. Prog. Ser. 86: 239–249.

Wikfors, G. H., J. W. Twarog & R. Ukeles, 1984. Influence of chemical composition of algal food sources on growth of juvenile oysters, *Crassostrea virginica*. Biol. Bull.167: 251–263.

Wikner, J. & A. Hagstøm, 1988. Evidence for a tightly coupled nanoplanktonic predator–prey link regulating the bacterivores in the marine environment. Mar. Ecol. Prog. Ser. 47: 137–145.

Yentsch, C. S. & J. H. Ryther, 1959. Relative significance of the net phytoplankton and nanoplankton in the waters of Vineyard Sound. J. Cons. Perm. Int. Exp. Mer. 24: 231–238.

Zar, J. H., 1984. Biostatistical analysis. Prentice Hall Inc. 718 pp.

Zeuthen, E., 1943. A cartesian diver micro-respirometer with a gas volume of 0.1 μl. Respiration measurements with an experimental error of 2×10^{-5} μl. C.R. Trav. Lab. (Carlsberg) 24: 479–518.