Bloom History of Picoplankter Aureococcus anophagefferens in the New Jersey Barnegat Bay-Little Egg Harbor System and Great Bay, 1995-1999

by

John B. Mahoney, Paul S. Olsen, and Dorothy Jeffress

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ABSTRACT

Comprehensive monitoring of the toxic picoplankter Aureococcus anophagefferens in eastern Long Island, NY, bays from 1986 through 2001 established its population dynamics and bloom histories in that region. This information supported research on various aspects of the species' chronic Long Island blooms. Similar monitoring for the species in the western or New Jersey side of the New York Bight, by contrast, lagged for over a decade. Minimal, albeit valuable, information on A. anophagefferens presence in that region was obtained by other researchers from single-occasion surveys along the northeast U.S. coast in 1988 and 1990. These surveys detected the species in New Jersey bays and ocean coastal waters from the Hudson-Raritan estuary south to Great Bay (approximately central on the New Jersey coast), and -- of greater portent -- found it in low-intensity bloom abundance in Barnegat Bay in 1988. Despite this warning, research attention to the phenomena in the New York Bight was focused almost exclusively on Long Island. Lack of a structured monitoring program in New Jersey specific for A. anophagefferens continued through 1997, which prevented sufficient documentation of the histories of major blooms in 1995 and 1997 in the Barnegat Bay-Little Egg Harbor system and Great Bay. To address this inadequacy, we conducted a pilot survey in 1998-1999 in the bloom center, with the cooperation of other agencies. Survey results, including the detailed history of a major bloom of A. anophagefferens in 1999, are presented in this report. Previously reported features of development of the 1995 and 1997 blooms in the study region, with some additional information, are re-examined and compared with the 1999 bloom history. Some characteristics of the New Jersey blooms are compared with those of well-studied Long Island blooms. This paper complements a previous report on the distribution of A. anophagefferens in the western New York Bight, including coastal waters of New Jersey and western Long Island.

KEY WORDS: Harmful algal blooms, Aureococcus anophagefferens, brown tide.

INTRODUCTION

Deleterious blooms in the New York Bight, so called "brown tides", of a coccoid 2-3 µm diameter picoplankter, described and named Aureococcus anophagefferens by Sieburth et al. (1988), were first observed in eastern Long Island bays in 1985. They recurred in the next two years, and subsequently in some years, and in varied loci in the region, through 2001 (Nuzzi and Waters, 2004). Their severe detriment to bay scallop (Argopecten irradians) and other components of the biota was recognized early (e.g., Bricelj and Kuenster, 1989; Dennison et al., 1989). Comprehensive monitoring of this picoplankter from 1986 through 2001 by the New York Suffolk County Department of Health Services (SCDHS) established its population dynamics and the histories of its blooms in affected bays, including the eastern-most Gardiners Bay-Peconic Bay system, and Shinnecock Bay, Moriches Bay, and Great South Bay on the Long Island southeastern shore (Nuzzi and Waters, 1989, 2004). This information prompted, and often was crucial to, extensive research on various aspects of the Long Island outbreaks. Despite the likelihood that A. anophagefferens also bloomed in Barnegat Bay, New Jersey, in 1985, 1986 and 1987 (Olsen, 1989), study of its blooms in the New Jersey side of the New York Bight was inadequately addressed for over a decade, and certain aspects of the blooms have yet to be examined.

A. anophagefferens presence in New Jersey coastal waters was unconfirmed until Anderson et al. (1989) reported a low abundance, 400 cells ml⁻¹, in a single archived September 1986 Barnegat Bay sample. Information on A. anophagefferens distribution in New Jersev coastal waters initially consisted of data obtained from single-occasion surveys along the northeast U. S. coast in 1988 and 1990, conducted to assess the range of the species beyond the eastern Long Island bloom center (Anderson et al., 1993). The authors warned that their results were limited due to the minimal sampling of individual locales. The 1988 survey southerly extent was Barnegat Bay at Manahawkin, New Jersey. A. anophagefferens levels of 3.5 x 10⁴ cells ml⁻¹ and 1.4 x 10⁵ cells ml⁻¹, respectively, were detected at two sites in southern Barnegat Bay. This detection of an A. anophagefferens bloom population, although of low intensity, may be especially important because the New Jersey samples were collected in late September, well past the typical time for the species' bloom development (May-June) in eastern Long Island (Bricelj and Lonsdale, 1997). The possibility of a much more intense population earlier in the year is suggested. The other 1988 survey New Jersey samples, these from the northern half of the bay, had levels of $<10^3$ cells ml⁻¹. Brownish water discoloration, evident when A. anophagefferens cell numbers are >2.0 x10⁵ ml⁻¹ (Nuzzi, personal communication), was not observed in Barnegat Bay in the summer of 1988 (Olsen, personal observation). Visible presence of the bloom population likely was masked because total pico-nanoplankton concentration approximated 2.0 x 10⁶ cells ml⁻¹, and the A. anophagefferens concentration when assessed at most made up only ~7.0% of the assemblage (Olsen, 1989). The 1990 survey ranged from Portsmouth, New Hampshire, to Chesapeake Bay. New Jersey samples were collected in late August, also after the typical primary bloom development period, and when Barnegat Bay water temperature likely was unfavorably high (at or close to annual peak ~28°C). Water temperatures >25°C are detrimental to A. anophagefferens (Nuzzi and Waters, 1989). Of the 10 New Jersey locales sampled, the species was detected in low concentrations (<216 cells ml⁻¹) in three Barnegat Bay locales, and ~16 km to the south in Great Bay; it was also present in comparable abundances in Sandy Hook Bay and two coastal ocean sites. It was not found

between Great Bay and Chesapeake Bay. In brief, with regard to New Jersey coastal waters, the surveys detected the species from the Hudson-Raritan estuary south to Great Bay and, more importantly, identified Barnegat Bay as a potential locus for its blooms. Anderson et al. (1993) concluded that the widespread distribution of *A. anophagefferens* they found in waters far from the eastern Long Island, NY, population "center" suggested that numerous of these areas have potential for its blooms, and they recommended ongoing monitoring for the picoplankter in these areas.

Light or epifluorescence microscopy is inadequate to reliably distinguish A. anophagefferens from similarly-sized, chloroplast-containing, picoplankton (Sieburth et al., 1988). As evidence of this difficulty, A. anophagefferens was initially misidentified as Nannochloris sp. when it bloomed in Long Island in 1985 (Nuzzi and Waters, 1989). Identification of the species for monitoring purposes was problematic until Anderson et al. (1989) provided an immunofluorescence method. Because this immunofluorescence methodology was not adopted for Long Island monitoring until 1988 (Nuzzi and Waters, 2004), accuracy of the Long Island 1985-1987 population-level and bloom-duration determinations is uncertain. Likewise, although tentatively identified as Nannochloris atomus, identity was not confirmed of the plankter dominant in 1985-1987 intense blooms in Barnegat Bay (e.g., 1.5 x 10⁶ cells ml⁻¹ in 1985); its gross morphology and size were similar to that of A. anophagefferens and its bloom water discoloration was yellow-brown (Olsen, 1989). A 400 cells ml⁻¹ A. anophagefferens concentration eventually confirmed in a sole archived 1986 Barnegat Bay sample (Anderson et al., 1989) points against dominance by the species. However, the sample was collected in September rather than typical bloom development time (May-June), was inadequately preserved (basic Lugol's Iodine), and was two years old when processed, so the enumeration could be grossly inaccurate or reflect a post-bloom collapse population.

In response to chronic occurrence of intense blooms of various pico- nanoplankton species in the Barnegat Bay-Little Egg Harbor system, and the threat of A. anophagefferens blooms, the New Jersey Department of Environmental Protection (NJDEP) in cooperation with the United States Environmental Protection Agency (USEPA) initiated a long-term phytoplankton surveillance of this system (Olsen, in USEPA, 1988-1999, inclusive). However, although recommended by the authors, an A. anophagefferens-specific monitoring program, patterned after Long Island's, was lacking in New Jersey when major blooms of the picoplankter occurred in the Barnegat Bay-Little Egg Harbor estuarine system and adjacent Great Bay in 1995 and 1997 (Nuzzi et al., 1996; Mahoney et al., 1997; Mahoney et al., 1999; Olsen and Mahoney, 2001). Consequently, establishment of the histories of these blooms was handicapped. To address the information paucity on A. anophagefferens bloom development in New Jersey, we conducted a limited survey for the species in the bloom center, primarily in 1998 and 1999. This permitted study of the development of a major bloom of the species in 1999; its detailed history is the main subject of this report. Previously reported features of development of the 1995 and 1997 New Jersey blooms, with some new information, are re-examined and compared with the 1999 bloom development. Some characteristics of the New Jersey and Long Island A. anophagefferens blooms are compared. This paper complements a previous report on the distribution during 1997-2001 of A. anophagefferens in the western New York Bight, from Delaware Bay to western Long Island, which included documentation of the first confirmed occurrence, in 1999, of a bloom of the species in New Jersey south of Great Bay (Mahoney et al., 2003b).

METHODS

Described in Chizmadia et al. (1984), Kennish (2001), and Hunchak-Kariouk and Nicholson (2001), the Barnegat Bay-Little Egg Harbor estuarine system (Fig. 1) is a shallow lagoon-type estuary, characteristic of the back-bay system of a barrier island coastline. Barnegat Bay extends ~48 km along the New Jersey coast, and is contiguous at its southern end with Manahawkin Bay which extends south ~6 km (for this report Manahawkin Bay will be considered to be part of Barnegat Bay). Little Egg Harbor extends to ~16 km south of Manahawkin Bay. Length of the combined system is ~70 km. Widths range from ~2.0 to 6.5 km. Depths range from an average of 1.3 m in the northern half of the system, to >2.0 m in Little Egg Harbor. The eastern portion, averaging <1 m in depth, is generally shallower than the middle and western portions which range to ~4.0 m deep. Greatest depths in Barnegat Bay, to 6 m, occur along the Intracoastal Waterway, a narrow channel traversing its length; ~73% of the bay is less than 2 m deep at mean low water. Water depths reach 7 m in southern Little Egg Harbor. Connection of the system to the Atlantic Ocean is at the northern end through the Bay Head-Point Pleasant Canal, and the Manasquan River; through Barnegat Inlet at the center; and through Little Egg Inlet at the southern end, which also connects to the Great Bay-Mullica River estuary. Tidal exchange in the central and northern portions is relatively restricted, and is somewhat greater in the southern portion. Primary exchange of ocean and bay water in Barnegat Bay occurs through Barnegat Inlet. The relatively small size of the inlet and the shallowness of the bay restrict tidal flow and attenuate tidal energy; tidal amplitude diminishes progressively north and south of the inlet. Freshwater input to Barnegat Bay and Little Egg Harbor primarily is along the western sides. Several major freshwater tributaries, the largest of which is Toms River at northern Barnegat Bay, enter along the northwestern perimeter; only a few creeks enter along the western perimeter in the southern half of the system. Numerous storm drains contribute fresh water runoff, either directly or through lagoons and tributaries. Freshwater input from ground water seepage has not been determined but appears to be substantial. Wind has a dominant role in circulation, which has a complex pattern. Periods of complete vertical mixing occur, particularly when wind velocities are high, although a tendency for two-layered circulation exists in areas deeper than 1.5 m. The proximity of the ocean causes a moderation of summer and winter temperatures. July and August are the warmest months, with a water temperature high of ~28°C, and January and February are the coldest, with a water temperature low of ~1°C. Water temperature changes can occur quickly in response to air temperature because of shallow depths. Atmospheric precipitation is well distributed over the system. Extra-tropical storms, especially from the northeast, may occur from September to March.

Great Bay is located ~1.5-3 km south of Little Egg Harbor; it is fed by the Mullica River. The Great Bay-Mullica River estuary is one of the few unpolluted estuaries in New Jersey; the basin is relatively free of domestic or industrial development, with most of the area being farmland or reasonably undisturbed pinelands and large tracts as undeveloped federal or state holdings (Durand and Nadeau, 1972). The physical character of Great Bay, a roughly funnel-shaped embayment, closely matches that of a "classic" estuary. Described in Charlesworth (1968), Durand and Nadeau (1972), and Able and Fahay (1998), Great Bay is 25 km long and has an average width of 4 km. It is generally shallow, having an average depth of 1.7 m at mean low water; deeper channels (to ~10 m) exist in and near Little Egg Inlet and the Mullica River. Fresh water input is primarily from the Mullica River, a major acid-water system, which drains a

large portion (1,476 sq. km) of the southern New Jersey Pine Barrens region. The bay mouth is constricted and partially blocked by sand bars and saltmarsh islands. The bay is connected to Little Egg Harbor through several salt-water creeks, and common tidal flow to the Atlantic Ocean at Little Egg Inlet (Fig. 1). Tidal circulation is counterclockwise; flood tides constitute the dominant flow with maximum strength at the north side of the bay and mouth of the Mullica River. Ebb currents prevail in the southern portion. The circulation pattern apparently abets retention of plankton in the bay, but during periods of high flow much of the bay water and consequently plankton are flushed out.

Survey of *A. anophagefferens* in the Barnegat Bay-Little Egg Harbor system and Great Bay initiated by the National Marine Fisheries Service (NMFS) James J. Howard Marine Sciences Laboratory (HL) primarily spanned 1998 and 1999; restricted monitoring was conducted in the next two years. Personnel of various agencies in New Jersey and New York concerned with harmful algal blooms in this region (the Interagency Committee on Phytoplankton Blooms in the New York Bight) provided assistance including study design, methodology training, sample collection, sample enumerations, and sample exchange for interlaboratory enumeration calibrations. Primary cooperating agencies included NJDEP, SCDHS, and USEPA.

The survey was pilot-study in character rather than a fully developed monitoring program. Neither the chosen sampling frequency nor sample site density was considered completely sufficient, but the monitoring scheme reflects the limits of available resources. Daily sampling recommended by Smayda (1995) was not feasible; his less desirable recommended frequency of once weekly was met during most of spring and throughout summer. The study region was divided into zones as recommended by Smayda (1995). These are designated southern, central and northern. The southern zone includes Great Bay to Barnegat Bay at Barnegat, NJ; the central zone includes Barnegat Bay from Waretown to Berkeley Island, NJ; and the northern zone includes Barnegat Bay from Seaside Park to Mantoloking, NJ (Fig. 1). Sampling site locations were based on previous phytoplankton surveys (Olsen, 1989; Olsen in USEPA, 1979-1999, inclusive). The study region base-map (Fig.1) showing positions of sample sites was prepared using a Geographic Information System (GIS). Great Bay is represented by one primary site (site 28). Primary sampling sites in southern and northern portions of Little Egg Harbor, respectively, are represented by sites 31, 32 and 33, 34, respectively. Primary sampling sites in Barnegat Bay are southern (sites 36, 37, 38), central (sites 40, 41, 43), and northern (sites 44, 46, 48). Supplementary samples were obtained by helicopter survey at six bay offshore sites (Fig. 1, identified as BB1, BB2 etc.) by USEPA, Region II. Most USEPA sampling sites complemented shore sampling sites in the same general area. A. anophagefferens incidence at coastal ocean sites during the survey period (Fig. 1, sites 35, 39, 45) was reported previously (Mahoney et al., 2003b).

Samples from shoreline sites were collected from docks with a Niskin bottle at ~ 0.5 m depth. USEPA sampling was with a Kemmerer bottle at ~ 1.0 m depth. Sampling through the water column was not done because of the shallowness of the system and the necessity to limit sample number. Water salinity and temperature measurements were made by personnel of various agencies using different means. Salinity was measured by a refractometer or Yellow Springs Instrument Co. meter; the values are expressed as practical salinity units (PSU), equivalent to parts per thousand $\binom{0}{00}$. Water temperature measurements were made variously by

meter (Orion Model 265; Hanna Model HI 9060) and thermometer. Climate data for Atlantic City, New Jersey, from 1998 were obtained from the National Climatic Data Center, Ashville, North Carolina.

Methods of sample handling, preservation, and immunofluorescence identification and enumeration of A. anophagefferens basically were those of Anderson et al. (1989, 1993); the immunofluorescence protocol included some minor modifications by J. Bredemeyer, SCDHS (SCDHS protocol; Bredemeyer, personal communication). In the processing of initial 1999 bloom samples at HL, A. anophagefferens cell aggregation in glutaraldehyde-preserved samples, which was most prevalent when cell concentrations were high and could advance during storage, frequently rendered enumerations highly inaccurate (Mahoney et al., 2003a). Therefore, all 1999 samples were reprocessed or newly processed using a cell disaggregation protocol (Mahoney et al., 2003a) prior to the immunofluorescence processing. In some instances such reprocessing resulted in extraordinary increase in cell counts. For example, in a representative group of samples there was: little change in enumeration of one; two- to 20-fold enumeration increases with several samples; and over 35-fold enumeration increase of one sample (Mahoney et al., 2003a). Besides its utility for enhancing count accuracy, in many instances the disaggregation protocol also resulted in detection of A. anophagefferens in samples in which it had previously been undetected; e.g., detection of abundances ≤ 100 cells ml⁻¹ in 10 of 12 samples of a February collection. Because of potential cell clustering, some of the cell abundances determined by SCDHS for the 1995 and 1997 New Jersey blooms using just the immunofluorescence protocol may be erroneously low. SCDHS processed 1995 New Jersey samples within a month of collection, and enumerated the 1997 New Jersey samples ~6 months after collection. Considerable cell aggregation can occur in month-old samples, and because this can progress with time, even greater cluster error is likely after six months of storage. SCDHS enumerations are identified by superscript SC. Archived 1997 and 1998 samples also were reprocessed or newly processed using the disaggregation protocol.

Based on data from irregular sampling in 1995, and improved but inadequate monitoring in 1997, the bloom scenarios we outline for these years are partly speculative. Reasonably comprehensive monitoring of the 1999 bloom supports greater confidence in its history, as reported. Basing conclusions about the population dynamics of the 1999 bloom on approximately weekly assessments is a study shortcoming of undetermined importance, however, given the reality that A. anophagefferens can double its population in a day (Dzurica et al., 1989), and a dense population of the species can collapse to pre-bloom levels in two or three days (see 1999 bloom history below). The monitoring scheme was adequate, we believe, to reveal general bloom development, but may not have been adequate to detect rapid population changes or spatially-limited abundance differences. The scheme ensured detection of bloom initiation and development in the spring of 1999, but likely was insufficient in the fall and early winter, when sampling frequency was decreased to twice monthly and a third bloom pulse occurred. Bloom areas showing greater or less A. anophagefferens population densities are delimited in Figures 1-24 following the common practice of extending the value obtained for a sample site approximately half way to adjacent sample sites. Consequently, bloom areas depicted in the figures are primarily illustrative rather than spatially accurate. Symbols delimiting areas of A. anophagefferens abundance in the map figures express an abundance gradient in the particular figure. Unless otherwise noted, environmental salinity and temperature values provided in this report are the geometric means of data for the study region zones.

Testing of toxicity of Long Island *A. anophagefferens* strains determined that this can vary depending on environmental conditions, or physiological state of the strain (Tracey et al., 1989). Also, *A. anophagefferens* toxicity can vary strain-to-strain, and a toxic strain can lose toxicity over time (Bricelj et al., 2001). A concentration as low as 3.5×10^4 cells ml⁻¹ of a highly toxic Long Island strain reduced feeding of juvenile hard clam (*Mercenaria mercenaria*), and $\geq 4 \times 10^5$ cells ml⁻¹ halted clam feeding (Bricelj et al., 2001). These concentrations will be referred to in discussion of *A. anophagefferens* abundances in New Jersey (either enumerated or calculated) and bloom effects.

RESULTS

A. anophagefferens Bloom History and Presence in the Study Region, 1995-1999

1995 A. anophagefferens Bloom Observations

An A. anophagefferens bloom in 1995 in the Barnegat Bay-Little Egg Harbor system and Great Bay, confirmed by SCDHS, was the first identified in the New York Bight in other than eastern Long Island, NY, bays. Its likely history was developed from various information sources. The bloom initially was detected in Tuckerton Bay, the southwestern-most portion of Little Egg Harbor (represented by sites 30, 31, Fig. 1), in the first week of May by biologist G. Zodl, at Biosphere Inc., a Tuckerton, NJ, aquaculture facility. Biosphere Inc. draws water from Tuckerton Bay for its culture system and in early May, coincident with presence of an intense picoplankton bloom in the bay, Zodl observed high mortalities of hard clam (M. mercenaria) larvae, and inhibition of feeding and growth of clam juveniles. By mid-May juvenile clam growth ceased entirely. Convinced of an association between the bloom and the observed effects, Zodl made light microscopy enumerations of picoplankton levels in the bay in June. His population assessments on June 5, 10, and 15, were 1.8, 1.5, and 1.1 x10⁶ cells ml⁻¹, respectively. Zodl described the picoplankton bloom as mono-clonal in appearance. However, what percentage of his counts represented A. anophagefferens is uncertain. Virtually monospecific Long Island A. anophagefferens blooms have been reported, but A. anophagefferens can cooccur with significant numbers of morphologically similar picoplankters, as well as other phytoplankton, during less intense blooms or during later bloom stages (Bricelj and Lonsdale, 1997). SCDHS, using immunofluorescence methodology, confirmed A. anophagefferens abundances of ~10⁶ cells ml^{-1 SC} in June Tuckerton Bay samples, which suggests Zodl's reported enumerations may approximate the actual population levels (as explained in the Methods section, SCDHS enumerations may have under-represented the population).

The bloom's full geographic distribution was not determined, but it was present at least in the southern half of Barnegat Bay, the western portion of Little Egg Harbor, and the northern portion of Great Bay (Fig. 1). The authors collected samples in the Barnegat Bay-Little Egg Harbor system and Great Bay on July 12, and USEPA, Region II, made a collection on August 23 which spanned the entire New Jersey intracoastal system from the Hudson-Raritan estuary to Delaware Bay. (Four samples were collected in the study region.) All six mid-July samples from Great Bay and the southern half of Barnegat Bay, encompassing approximately 32 km, contained *A. anophagefferens* in concentrations ranging ~2.7 to 4.5 x 10⁵ cells ml^{-1 SC}. The four

study region samples from the USEPA collection had levels $\leq 2 \times 10^3$ cells ml^{-1 SC}. Available *A. anophagefferens* population abundance data, and the observed detrimental effects on Biosphere Inc. cultured clams, suggests that duration of the bloom was at least all of May through mid-July. *A. anophagefferens* population levels in southern Barnegat Bay and Great Bay in mid-July, lower by 50% or more than the confirmed June level, suggest that the bloom was waning at this time. Low *A. anophagefferens* abundance in August ($\leq 2 \times 10^3$ cells ml^{-1 SC}) shows the bloom had collapsed between mid-July and then. Total pico-nanoplankton abundance in the southern half of the system at this time was $\geq 2 \times 10^6$ cells ml⁻¹, so the pico-nanoplankton assemblage was overwhelmingly dominated by other species.

If complete cessation of clam growth at Biosphere Inc. in mid-May is used as an indicator, and the cellular toxicity of A. anophagefferens then blooming in Tuckerton Bay is assumed to have been comparable to or less than that of a highly toxic Long Island strain (Briceli et al., 2001), the A. anophagefferens population at this time can be inferred to have been at least 4 x 10⁵ cells ml⁻¹. Extrapolation back from this population level to a hypothetical over-winter level of $\sim 2 \times 10^3$ cells ml⁻¹, assuming A. anophagefferens growth rates of 0.46 or 0.77 doublings per day at 13°C or 19°C, respectively (based on growth rates of Cosper et al., 1989, and water temperatures typical in our study region in late April through the first week of May, and the second week of May, respectively, in 1998, 1999), places bloom initiation approximately two weeks earlier. If the over-winter level was $\sim 10^2$ cells ml⁻¹ (the March 1999 level), initiation could have been in mid-April. Partial recovery of surviving Biosphere Inc. cultured clams in early July, and an apparent complete growth recovery by mid-July observed by Zodl, are noteworthy given that the July 12 Tuckerton Bay A. anophagefferens level was $\sim 2.8 \times 10^5$ cells ml^{-1 SC}. A temporary waning of the bloom in the area earlier in the month, followed by renewed development, is one possible explanation for the clam recovery. Lower cellular toxicity of the New Jersey strain(s) is another possibility. Data are lacking to support or refute either of these possibilities.

Pico-nanoplankton Presence in 1996, an *A. anophagefferens* Non-Bloom Year

A. anophagefferens did not bloom in the study region in 1996, and its detected concentrations were low; at least some pico-nanoplankton spp. were favored in the Barnegat Bay-Little Egg Harbor system, however (Table 3, Olsen and Mahoney, 2001). Exclusive of A. anophagefferens, pico-nanoplankton bloom peaks occurred in mid- to late August, when water temperatures generally were at or near annual maximum (~28°C). In southern Barnegat Bay, typically high total pico-nanoplankton levels evident in previous years continued, with the highest abundance (3.1 x 10⁶ cells ml⁻¹) observed for an entire 11 year survey span (1987-1998) found in late August. However, perhaps suggesting suitability of conditions for fewer pico-nanoplankton species or an unusual species assemblage, mean chlorophyll level for southern Barnegat Bay in 1996 was ~10 to 54 percent less than in all the NJDEP survey years prior. Definitely unusual was that pico-nanoplankton abundance was higher in northern Barnegat Bay in 1996 than in 1987 through 1995.

1997 A. anophagefferens Bloom History

In 1997, tracking of development of the second confirmed *A. anophagefferens* bloom in the Barnegat Bay-Little Egg Harbor system and Great Bay was improved by increased monitoring, permitted by SCDHS agreement to process New Jersey samples on a regular basis. Collections were made approximately weekly from mid-May through August, primarily at many of the sites shown in Fig. 1. Approximately half of the sampling was done by NJDEP and NMFS personnel from shore sites; USEPA accomplished the balance. Additional samples from various routine shore sites were collected irregularly before, during, and after the primary collection effort, including collections in October and December. Occasionally sampling was done at sites other than routine ones. The total of New Jersey samples SCDHS eventually was able to process was limited due to ongoing intensive monitoring of eastern Long Island bloom loci. Nevertheless, the likely history of this *A. anophagefferens* bloom is based primarily on SCDHS population estimates. Beginning in 1999, samples not enumerated by SCDHS, as well as available archived 1997 SCDHS-processed water samples, were newly processed or reprocessed at HL, and this provided considerable additional information.

Three previously unprocessed samples collected on April 17 from central Little Egg Harbor and southern and northern Barnegat Bay, respectively, had A. anophagefferens abundances of 4.3, 1.4, and 0.45 x 10⁶ cells ml⁻¹, respectively. Four or more processing's using improved methodology (Mahoney et al., 2003a) affirmed accuracy of these enumerations. The bloom's mid-April possible distribution (which is especially speculative due to the low number of samples), with decreasing cell abundance from south to north, is depicted in Fig. 2. The high cell concentrations in the three samples from relatively widely separated locales support suspicion of population growth rather than passive cell concentration. Extrapolation from the highest mid-April abundance to a possible over-winter level of 2 x10³ cells ml⁻¹ (average level was only 1.5×10^2 cells ml⁻¹ in March 1998), using A. anophagefferens growth rates of 0.3 or 0.4 doublings per day at 10°C or 12°C, respectively [(Cosper et al., 1989); the water temperatures were typical in our study region in March and April 1998, 1999], suggests that initiation of the bloom could have been in the first half of March. The high cell abundances detected for this time of year are noteworthy, as is the moderately high bloom population in northern Barnegat Bay. (Available information suggests the northern zone does not characteristically support high abundance of the species.) Population levels at this time in Great Bay were not determined.

The initial pulse waned drastically over the next several weeks (no information is available on the pattern of decline). During mid- to late May, population abundances at sites from Little Egg Harbor to northern Barnegat Bay ranged just from 2×10^3 to 7.6×10^4 cells ml⁻¹. All zones shared higher levels, although southern Barnegat Bay (site 37) had the highest level. *A. anophagefferens* abundance in Great Bay was not assessed then. The population was generally decreased in the first week of June; sites in southern Barnegat Bay and mid-Little Egg Harbor (33, 37) had the highest levels (~ 3.4 -4 x 10^4 cells ml⁻¹, respectively). A second bloom pulse then developed for approximately a week, and by mid-June was distributed through most of the Barnegat Bay-Little Egg Harbor system and in Great Bay. The second pulse apparently achieved peak intensities in mid-June. Bloom distribution, from a composite of maximum levels obtained from June 11 and June 17 samples, is provided in Fig. 3. Levels in this period of $\geq 1.5 \times 10^5$ cells ml^{-1 SC} were detected at 11 sites from central Barnegat Bay south to Great Bay; the northernmost site sampled, Barnegat Bay at Mantoloking, had the lowest *A. anophagefferens*

presence ($<10^3$ cells ml⁻¹). The highest concentration, $\sim 6 \times 10^5$ cells ml^{-1 SC}, was in the northern half of Little Egg Harbor (site 33); this locus was bracketed north and south (sites 31, 42) with concentrations of ~ 1.5 -3 x 10^5 cells ml^{-1 SC}. Great Bay levels were ~ 2 -3 x 10^5 cells ml^{-1 SC} at two inner bay sites (sites 27, 28), and $\sim 7 \times 10^4$ cells ml^{-1 SC} at another (site 29). Varied mid-June cell abundances in Little Egg Harbor and Great Bay (Fig. 3) likely reflect patchy bloom development. The second pulse abundance maxima were far below levels in the first pulse; to what extent this reflects enumeration methodology difference or actual population difference is unknown. This pulse declined in the second half of June.

With the exception of a minor third bloom pulse in the first half of July (restricted to Little Egg Harbor) which reached ~1-3 x 10⁵ cells ml⁻¹, levels detected during this month were <5 x 10⁴ cells ml⁻¹. (All samples collected in July through the remainder of the year were reprocessed or newly processed at HL.) August levels primarily were <3 x 10⁵ cells ml⁻¹; a Little Egg Harbor site (33) had the most abundance, $\sim 10^4$ cells ml⁻¹. Presence of A. anophagefferens was detected at all Barnegat Bay, Little Egg Harbor, and Great Bay sample sites in October and December. In October, levels reached as high as 10⁴ cells ml⁻¹ in certain southern and central zone sites (32, 36, 43), and were $< 5 \times 10^3$ cells ml⁻¹ elsewhere in the study region. In December, levels of 1-3 x 10⁴ cells ml⁻¹ were detected in south or central Barnegat Bay locales (sites 38, 43), and 10⁴ cells ml⁻¹ in a Little Egg Harbor locale (site 34); all locales were on the western side of the system. Levels at other sites were $<4 \times 10^3$ cells ml⁻¹. Note that Little Egg Harbor was part of the locus of development for the first two bloom pulses, and the third pulse occurred there exclusively. The southern zone retained the greatest suitability for sustaining the A. anophagefferens bloom, even in July when other pico-nanoplankton species were in high abundance (Fig. 2, in Olsen and Mahoney, 2001). Salinities in May through August in the southern and central zones were >26 PSU. Northern zone salinity (data are too few to provide means) predominantly ranged ~17-23 PSU in May through August; the exception was a temporary increase to 25 PSU in the third week of August. Available water temperature data are too few to consider.

Pico-nanoplankton Presence in 1998, an *A. anophagefferens* Non-Bloom Year

In 1998, the first year of the HL survey, primary sampling for *A. anophagefferens* in the survey region was once monthly in January through March and October through December, twice monthly in April, May and September, and weekly in June through August. USEPA helicopter collection of bay offshore samples was limited to the middle and end of July because no *A. anophagefferens* bloom developed. In January, *A. anophagefferens* was detected at all sites (Fig. 1). Its population levels varied little from December 1997 levels, with some higher and some lower; the same concentration as in December, 1997 (3 x 10^4 cells ml⁻¹) persisted at one locale (site 38) in central Barnegat Bay. In February, levels in Barnegat Bay and Little Egg Harbor predominantly were $\leq 2 \times 10^3$ cells ml⁻¹, with presence at all locales except northernmost Barnegat Bay (site 48); greatest abundance (5 x 10^3 cells ml⁻¹) was in northern Little Egg Harbor. In March, population decline throughout the study region reduced levels to $\leq 3 \times 10^2$ cells ml⁻¹ at half of the sites, and below level of detection at the remainder. Slight population increase began in early April, and by late April *A. anophagefferens* apparently was present throughout Barnegat

Bay and Little Egg Harbor. Greatest abundances (1-3 x 10^3 cells ml⁻¹) were in Little Egg Harbor and southern Barnegat Bay; levels were ≤ 7 x 10^2 cells ml⁻¹ elsewhere in the system. Despite the presence of this seed population, a bloom did not develop. The overall population instead declined in the first half of May so that by mid-month, when bloom development would be expected given suitable conditions, maximum abundance was only $\sim 10^3$ cells ml⁻¹. The population peak for the year was 10^4 cells ml⁻¹ in mid-June at a northern Little Egg Harbor site (site 34). Otherwise, abundances of $\geq 10^3$ cells ml⁻¹, present at most sites in the system, continued in June through mid-July. Study region levels were $< 10^3$ cells ml⁻¹ through the rest of the year. The Little Egg Harbor and southern Barnegat Bay region consistently was the most favorable locus. The species was absent, or in concentrations below detection, primarily in central and northern Barnegat Bay.

1999 A. anophagefferens Bloom History

Primary sampling in 1999 was at twelve shoreline sites (Fig. 1), once monthly in January through March, twice monthly in April and September through December, and weekly in May through August. Collections by USEPA provided offshore bay samples from six sites (Fig. 1), approximately weekly from late May through August.

In January through March, A. anophagefferens was present at most sampling sites, in levels of <100 cells ml⁻¹; the population did not increase noticeably during this period. During the first three weeks of April, abundances in southern Barnegat Bay and Little Egg Harbor (sites 30-37, Fig. 4; the area encompassed by these sites is considered the bloom primary locus), increased to ~1-2.5 x 10³ cells ml⁻¹; concentrations elsewhere in the system were <300 cells ml⁻¹. A composite of distribution and cell concentration for the period is shown in Fig. 4. Accelerated late April-early May population increase in the bloom primary locus produced abundances of ~5 x 10³ to 3.5 x 10⁴ cells ml⁻¹; concentrations were <10³ cells ml⁻¹ at the other locales (Fig. 5). By mid-May, population growth in the bloom primary locus, and part at least of Great Bay (site 28), estimated to be as much as one doubling per day, resulted in population abundances ranging from $\sim 2 \times 10^5$ to 2×10^6 cells ml⁻¹; greatest density was in southwestern Little Egg Harbor (site 31) (Fig. 6). A population increase to $\sim 6 \times 10^3$ cells ml⁻¹ just northward of the bloom primary locus (i.e., site 38) suggested bloom incipient northward expansion (Fig. 6). Bloom initiation was not apparent in the central and northern zones in mid-May, despite presence of A. anophagefferens. In the following week, population levels in much of the bloom primary locus were unchanged, but population increase in the northern part of the southern zone and in the southern central zone evidenced northward expansion of the bloom. Abundance in Great Bay (site 28), however, was reduced by more than an order of 10 from the previous week's level (Fig. 7). At the end of May the population had decreased in southern Little Egg Harbor (site 31) by \sim an order of 10, and greater population density (6 x 10⁵-1 x 10⁶ cells ml⁻¹) had shifted northward in Little Egg Harbor (site 33), and to southern Barnegat Bay (sites 36, 37). The population in Great Bay showed recovery (Fig. 8). Throughout May, the bloom did not develop in the northern two thirds of Barnegat Bay (sites 42-49, Fig. 8), where A. anophagefferens levels did not exceed 9 x 10^3 cells ml⁻¹, and primarily were $< 5 \times 10^2$ cells ml⁻¹. Wide variation of population levels at various bloom development loci through the month suggests partly ephemeral development. That is, a bloom development locus remained consistently favorable overall, but population

abundances in particular portions sometimes varied greatly. Illustrating this is the relatively low abundance ($\sim 9 \times 10^3$ cells ml⁻¹) in late May at an offshore Little Egg Harbor site (site 30), but a level of $\sim 3 \times 10^5$ cells ml⁻¹ at a close-by inshore site (site 31; Fig. 8).

The bloom pulse intensified in early June (Fig. 9). Most bloom primary locus cell abundances were increased to 1-2.4 x 10⁶ cells ml⁻¹, and the areas of greater abundance were more widespread there than in late May. Patchy development in Little Egg Harbor is suggested by one site (33) having a population of only $\sim 4 \times 10^4$ cells ml⁻¹, whereas nearby sites (31, 34) had a level of $\sim 10^6$ cells ml⁻¹. Northward of the bloom primary locus, a population of 8 x 10^5 cells ml⁻¹ ranged into central Barnegat Bay. Development in Great Bay resulted in levels of 1-5 x 10⁵ cells ml⁻¹. The population then declined in Barnegat Bay and northern Little Egg Harbor so that by mid-June cell abundances were considerably reduced; the population increased, however, in the western side of southern Little Egg Harbor (site 31) (Fig. 10). The bloom primary locus continued to be southern Barnegat Bay and Little Egg Harbor; here, the higher cell abundances found a week earlier were still present but were less widespread. Again, relatively low population levels at some bloom primary locus sites (30, 33) were found adjacent to others where high population levels were detected (sites 31, 32, 34). The bloom at mid-June extended into the lower northern zone (site 44); this was the limit of its northward expansion during the month. The bloom did not wane in western Great Bay and instead by mid-month evidenced an apparent population ~doubling to 10⁶ cells ml⁻¹.

A second bloom pulse (the population growth resurgence is considered to have been sufficient to warrant a pulse designation) developed in the Barnegat Bay-Little Egg Harbor system in the third week of June (Fig. 11). *A. anophagefferens* abundances in southern Barnegat Bay and the eastern side of Little Egg Harbor were ~ 4 x 10⁶ cells ml⁻¹; the remainder of the bloom primary locus had levels of 2-3 x 10⁶ cells ml⁻¹. Levels in Great Bay and central Barnegat Bay were relatively unchanged from those in mid-June. Decline of this pulse in Barnegat Bay and Little Egg Harbor apparently began in the last week of June, evidenced by system-wide reduction of population levels, although bloom population distribution had not diminished. At this time water color of the southern and central zones was brownish, characteristic of *A. anophagefferens* blooms of at least moderate intensity; mean Secchi depth in these zones was 0.3 m. Bloom primary locus maxima were decreased to ~1-2 x 10⁶ cells ml⁻¹ by the end of the month (Fig. 12). A disconnect between bloom development in Great Bay and the Barnegat Bay-Little Egg Harbor system was evidenced by the Great Bay population showing little change during the second bloom pulse in the Barnegat Bay-Little Egg Harbor system. (A previous instance of such disconnect was apparent in ~mid-May, Figs. 6, 7).

Collapse of the Barnegat Bay-Little Egg Harbor second bloom pulse population and of the Great Bay population was complete by the end of the first week of July, although *A. anophagefferens* distribution remained approximately the same as in late June (Fig. 13). Likely reflecting the *A. anophagefferens* bloom collapse, mean Secchi depths then were increased to 0.5 m or 0.6 m, respectively, in the southern and central zones. Southern Barnegat Bay continued to have greatest cell abundance, but this was decreased by ~two orders of 10 from the level in the previous week. At mid-July, the population showed further system-wide decrease (Fig. 14). Eastern Manahawkin Bay (site 36) in the southern zone then had the most cell abundance, ~4 x 10^3 cells ml⁻¹ -- only ~one fifth of the early July level. The population maintained the same distribution, but had slightly lower abundance, in the third week of July (Fig. 15). Only minor population changes -- either increases or decreases -- were evident at the end of the month;

western Manahawkin Bay (site 37) and, uncharacteristically, northern Barnegat Bay at Mantoloking (sites 48, 49), had the highest population level (\sim 3 x 10³ cells ml⁻¹; Fig. 16). Through August, *A. anophagefferens* was present at all sites; cell abundances, reflective of survival but little or no population growth, primarily were \leq 1 x10⁴ cells ml⁻¹, and never exceeded 2 x10⁴ cells ml⁻¹. No study region zone appeared more suitable than the other.

A third bloom pulse initiated in the southern zone in early September (Fig. 17). This pulse spanned September through the end of the year, and was characterized by temporal and spatial waxing and waning. Highest early September abundances, 4-6 x 10³ cells ml⁻¹, were in eastern Little Egg Harbor (site 32), southern Barnegat Bay (sites 36, 38), and a central zone locale (site 43). Development during September brought abundances in Little Egg Harbor and southern Barnegat Bay (bloom primary locus: sites 30-37) to ~7-15 x 10³ cells ml⁻¹; northward in the system, however, there was a general population decrease from levels earlier in the month (Fig. 18). Comparison of the geometric means of cell abundances at three sites (32, 34, 36) in Little Egg Harbor and southern Barnegat Bay in early and late September suggests population growth in September approximated 0.1 doubling per day.

Similar comparison of late September to early October cell abundances in northern Little Egg Harbor (site 34), apparently the most suitable locale for *A. anophagefferens* in early October, suggests growth of \sim 0.4 doubling per day to achieve a population of 3 x 10⁵ cells ml⁻¹. (Water temperature ranged from \sim 19 to 21°C.) A southern central zone site (40) then had the second-most abundance, 5 x 10⁴ cells ml⁻¹. Levels in the rest of the study region were \leq 1.5 x 10⁴ cells ml⁻¹; the lowest abundances were in the northern half of Barnegat Bay, southwestern Little Egg Harbor and Great Bay (Fig. 19). Continued bloom development during October raised levels in northern Little Egg Harbor and southern Barnegat Bay to 0.7-2 x 10⁵ cells ml⁻¹ (Fig. 20). Development extended northward through most of Barnegat Bay, although cell abundances in general were progressively decreased to the north (Fig. 20). The early October relatively high population in part of Little Egg Harbor was \sim halved by the end of the third week.

Most of the third bloom pulse development was in the central zone in November. In early November (Fig. 21), the higher A. anophagefferens concentrations $(1.1\text{-}1.3 \text{ x } 10^5 \text{ cells ml}^{-1})$ were in the central zone, and the southern zone Little Egg Harbor and southern Barnegat Bay population was decreased greatly to levels of $\leq 1.5 \text{ x } 10^4 \text{ cells ml}^{-1}$. The least favorable areas at this time were northern Barnegat Bay and southern Little Egg Harbor. By late November, depending on the locale, the central zone population had increased \sim two-fold to as much as \sim 17-fold (Fig. 22). Ten-fold population increase just southward (site 38) caused the region of highest abundance to include the contiguous part of the southern zone. The A. anophagefferens population in Little Egg Harbor was much decreased from the already low levels present early in the month. In early December (Fig. 23), the higher population abundances continued in the central zone. Levels in the northern zone basically remained as previous; initiation of population increase was evident in Little Egg Harbor. By late December, bloom development had shifted south so that there was decline in the northern central zone and increase in the southern zone. Maximum cell densities at this time were greatly increased over those early in the month, and found predominantly in the southern zone (sites 34, 36, 38, 40; Fig. 24).

Summary of A. anophagefferens 1995, 1997, 1999 Bloom Distribution

The 1995 bloom was present at least in the southern half of Barnegat Bay, the western portion of Little Egg Harbor, and the northern portion of Great Bay; its full geographic distribution was not determined. The 1997 bloom apparently was initially distributed throughout the Barnegat Bay-Little Egg Harbor system; its presence at that time in Great Bay is unknown. After this initial pulse waned, a second pulse developed through most of the Barnegat Bay-Little Egg Harbor system and Great Bay. A minor third pulse was restricted to Little Egg Harbor. In 1999, the initial bloom pulse was present first in southern Barnegat Bay and northern Little Egg Harbor (bloom primary locus), and later developed northward and southward in parts of central Barnegat Bay and Great Bay, respectively. A second pulse initiated in the bloom primary locus, and as before eventually encompassed central Barnegat Bay and Great Bay. A third pulse initiated in the bloom primary locus; development primarily was in the central zone, coincident with population decline in the southern zone and, finally, third pulse development shifted southward, with population increase in the southern zone and decline in the northern central zone.

Summary of A. anophagefferens 1995, 1997, and 1999 Bloom Dynamics

The 1995 *A. anophagefferens* bloom possibly initiated in the second half of April; by mid-May the population was intense enough (e.g., $\geq 4 \times 10^5$ cells ml⁻¹) to halt feeding of cultured hard clam juveniles in the Tuckerton Bay portion of Little Egg Harbor. When the bloom peaked was not established; June levels of $\sim 10^6$ cells ml⁻¹ were confirmed. Bloom waning likely began in the first half of July; when the bloom collapsed completely is unknown (likely in the second half of July). In 1997 the initial bloom pulse possibly initiated in the first half of March. Peak population abundance during this pulse likely was in April. It waned through early June. A second pulse developed in the second week of June, and began a decline a week later. A third pulse restricted to Little Egg Harbor developed in the first half of July, and collapsed by the end of the month.

Waxing and waning, with both spatial and temporal components, was a recurrent feature of the 1999 bloom; it had several distinct pulses, as did the 1997 bloom. The first pulse initiated in late April-early May, developed through mid-May, and in the remainder of May population levels in particular areas variously remained the same, declined, or intensified. After this complex phase, the initial pulse intensified in the first week of June throughout the study region, particularly in the southern and central zones, then declined in most areas in mid-June. A second bloom pulse developed in the third week of June, attained in some locales the highest cell abundances found in the survey (equivalent to the highest found in the 1997 bloom), and collapsed in the first week of July. A third pulse initiated in early September and developed in November and December in the Barnegat Bay-Little Egg Harbor system, with a partial shift of the development locus over several weeks from the central zone to the southern zone. Peak abundances of the 1997 bloom were in the first pulse, and peak abundances in 1999 were predominantly in the second pulse.

General Features of the Study Region Pico-Nanoplankton Assemblage

NJDEP, with the cooperation of USEPA, surveyed the phytoplankton of the Barnegat Bay-Little Egg Harbor system from 1987 through 1998 (Olsen, 1989; Olsen in USEPA, 1988-1999, inclusive; Olsen and Mahoney, 2001). Coccoid pico-nanoplankton 1.5-3.5 (occasionally 4.5) µm in diameter, seasonally (mid- to late summer) dominated the phytoplankton throughout the system. They seasonally numerically comprised at least 75% of the total phytoplankton, and were 90-99% during their bloom maxima. Phytoplankton diversity was considerably greater when and where pico-nanoplankton spp. were not dominant. Despite the system-wide piconanoplankton dominance, three zones -- northern, central, and southern -- could be delineated on the bases of phytoplankton composition and abundance. The northern zone had considerable diatom and phytoflagellate components of the phytoplankton assemblage which sometimes resulted in higher biomass; little other than pico-nanoplankton (primarily *Nannochloris atomus*) were prominent in the southern zone. The three areas remained distinct on the basis of relative phytoplankton abundance, even when pico-nanoplankton blooms, e.g., in 1987, were prevalent. Southern zone pico-nanoplankton blooms then were the most widespread, began earlier (mid-to late June), continued considerably longer with sustained high abundances (>5 x 10⁵ cells ml⁻¹ to >1.2 x 10⁶ cells ml⁻¹), and lasted later in the year (to early October) than in the central and northern regions. Pico-nanoplankton concentrations in the southern zone greatly exceeded those in the northern zone in five of the six years in which phytoplankton populations in these regions were compared; levels were approximately equal in one year. In 1987, maximum southern zone pico-nanoplankton abundance was 1.34 x 10⁶ cells ml⁻¹ in late August, and 1.49 x 10⁶ cells ml⁻¹ in early October, whereas pico-nanoplankton in the northern and central zones attained much lower peak levels (>5 x 10⁵ cells ml⁻¹); the blooms in these zones were of shorter duration, persisting only from late July to early September. A direct relationship was found between piconanoplankton abundance and salinity. The southern region had higher prevailing salinity, and the northern area a lower salinity regime due to greater freshwater inputs. Greatest variation of salinity and pico-nanoplankton abundance occurred in the northern and central portions of the system. General pico-nanoplankton bloom development was associated with water temperatures >20°C, and >25°C at peak levels.

Pico-nanoplankton ascendancy in the system apparently has increased in recent decades. Comparison of phytoplankton assemblages reported by Mountford (1971) and those found subsequently in the NJDEP surveys (cited above) reveal major change in abundance and distribution of phytoplankton. Although an abundance in summer of ultraplankton (1-3 μm in size) forms reported by Mountford (1971) has remained a consistent feature of the system for decades, maximum pico-nanoplankton cell densities found in the NJDEP surveys ranged from 1.5 to 4.0 times greater than those found in the earlier studies. Moreover, abundance and diversity of larger species, particularly dinoflagellates, were comparatively reduced in the presence of persistently high pico-nanoplankton abundance. That is, Mountford (1971) observed an abundance of ultraplankton, which he believed were predominantly *N. atomus*, to be "superimposed on the normal phytoplankton community", whereas the later surveys indicate that the former "normal" community largely has been displaced by the pico-nanoplankton as well as the occurrence of phytoflagellate blooms reported by Mountford were rarely observed during the NJDEP surveys.

Similarity of Phytoplankton of Study Region and Great South Bay, Long Island

N. atomus was commonly the most numerous component of the phytoplankton in much of the western New York Bight coastal waters, including the Hudson-Raritan estuary, during two decades of surveys (Olsen, in USEPA, 1979 to 1999, inclusive; Olsen and Cohn, 1979). This species and various other pico-nanoplankton spp. were most abundant in summer and early autumn, but associated larger phytoplankton often had high abundance. Phytoflagellates dominant in frequent spring and summer blooms included Heterosigma akashiwo (initially identified as Olisthodiscus luteus); Katodinium rotundatum; Prorocentrum spp.; diatoms including Skeletonema costatum and Thalassiosira spp. typically were abundant from late summer through spring.

The phytoplankton assemblage in the Barnegat Bay-Little Egg Harbor system is much less diverse than that of other western New York Bight coastal waters surveyed. Characteristically having pico-nanoplankton dominance during late spring to early fall, usually with N. atomus in greatest abundance and several other pico-nanoplankton species having subdominant or successional importance (Olsen, in USEPA, 1979 to 1999, inclusive; Olsen and Mahoney, 2001), this system's phytoplankton assemblage particularly resembles that of Great South Bay, where N. atomus and a few other pico-nanoplankton species including A. anophagefferens generally have numerically dominated for decades (Lively et al., 1983; Nuzzi and Waters, 1989). During 1985 through 2002, the phytoplankton of Great South Bay with few exceptions always consisted of cells smaller than 10 µm (Nuzzi and Waters, 2004). Long Island A. anophagefferens bloom loci and the Barnegat Bay-Little Egg Harbor system have common features, conforming largely to the characterization of "bloom sensitive waters" by Paerl (1988), including limited circulation, generally shallow depths with enhanced warming, allochthonous loadings from intense development in adjacent areas, and trophic interactions which help sustain pico-nanoplankton populations. However, the Long Island South Shore estuary (in particular Great South Bay) may share with the Barnegat Bay-Little Egg Harbor system an especial suitability for A. anophagefferens blooms. The last A. anophagefferens bloom in the Long Island Peconic system was in 1995, but A. anophagefferens blooms persisted in the South Shore estuary through 2001 Nuzzi and Waters, 2004; Nuzzi personal communication).

A. anophagefferens Known Bloom Effects, and Apparent New Jersey Strain Toxicity

A. anophagefferens blooms in eastern Long Island bays, which typically developed coincident with the spawning, larval development, and juvenile growth periods of various bivalves, caused adverse effects on larval and adult stages of suspension-feeding bivalves, including, e.g., recruitment failure of bay scallop (A. irradians) (Bricelj and Lonsdale, 1997). Growth reduction of eelgrass (Zostera marina) through light attenuation, most pronounced when an A. anophagefferens bloom overlapped the eelgrass March-May peak growing season, was another major A. anophagefferens bloom detrimental effect in Long Island (Dennison et al., 1989).

As already mentioned in the Methods section, *A. anophagefferens* toxicity can vary depending on a number of factors, such as the particular strain and its physiological state (Bricelj et al., 2001). Evidencing the consistently toxic nature of the 1995, 1997, and 1999 *A*.

anophagefferens blooms in New Jersey is the reported high mortality of cultured hard clam (*M. mercenaria*) larvae, and severe inhibition of juvenile clam growth, at Biosphere Inc. during the 1995 bloom, and feeding inhibition and growth cessation in juvenile clams in this and a second aquaculture facility in the same area over 6-8 week periods during the 1997 and 1999 blooms. These deleterious effects were not observed when *A. anophagefferens* did not bloom. Effects on natural bivalve populations of 1995-1999 *A. anophagefferens* blooms in the Barnegat Bay-Little Egg Harbor system and Great Bay were not determined. Only one New Jersey *A. anophagefferens* isolate has been established (Center for Culture of Marine Phytoplankton, strain CCMP1794), and its toxicity has not been tested. Its toxicity will be assessed in the near future and compared with toxicity of Long Island strains (Bricelj, personal communication).

DISCUSSION

Following the 1985 A. anophagefferens blooms in multiple eastern Long Island bays (Nuzzi and Waters, 1989), in Narragansett Bay, RI (Smayda and Villareal, 1989), and possibly Barnegat Bay, NJ (Olsen, 1989) there were recurrences in Long Island in the next two years, and in some subsequent years, with varied location, intensity, and duration to 2001 (Nuzzi and Waters, 2004). In the New Jersey center picoplankter blooms suspected to be of A. anophagefferens recurred in 1986 and 1987 (Olsen, 1989), and there were the confirmed A. anophagefferens blooms in the 1990s discussed in this report, as well as occurrence into the current decade. The 1985 A. anophagefferens bloom in Narragansett Bay apparently was anomalous because none has occurred there since. Research on A. anophagefferens blooms in the New York Bight focused on those in Long Island, with less attention accorded to the 1985-1987 blooms, and even the confirmed and reported 1995 bloom (references cited above), in New Jersey than to the single occurrence in Rhode Island. An apparent absence of A. anophagefferens blooms in New Jersey waters from 1989 through 1994 (Olsen and Mahoney, 2001) possibly contributed to this inattention. Major confirmed blooms in 1995, 1997, and 1999 in the New Jersey Barnegat Bay-Little Egg Harbor system and Great Bay, however, ensured classification of this region as an A. anophagefferens bloom center. The New Jersey A. anophagefferens blooms, and occurrences in Delaware and Maryland in the last decade (Nuzzi and Waters, 2004), demonstrate the merit of the conclusion by Anderson et al. (1993) that numerous areas far removed from the Long Island, NY center have the potential for deleterious blooms of the species.

The likely history of the 1995 *A. anophagefferens* bloom in the Barnegat Bay-Little Egg Harbor system and Great Bay was constructed from limited population enumerations and circumstantial evidence. Tracking of the 1997 *A. anophagefferens* bloom was improved but also insufficient to provide a complete history. Although sparse, the information we report is the extent of documentation on these blooms. Our survey provided a more rigorous tracking of 1999 *A. anophagefferens* bloom development. The sampling scheme was sufficient, we believe, to provide at least general bloom dynamics information. Temporal and spatial sampling gaps, potential relatively rapid growth of *A. anophagefferens*, or catastrophic collapse of a bloom population introduced actual or potential limitations; nevertheless, the survey results are profoundly superior to the information obtained for the 1995 and 1997 blooms. The survey provided year-round tracking of the population through two years, and the first reasonably

complete history of an *A. anophagefferens* bloom in the study region. The survey identified the main locus of *A. anophagefferens* bloom development in the study region in 1999 to be Little Egg Harbor and contiguous southern Barnegat Bay. Adding to the latter finding, in 1997 Little Egg Harbor was part of the locus of development for two bloom pulses, and a third bloom pulse developed there exclusively. Also, greatest abundance of *A. anophagefferens* in 1998, a non-bloom year, was in Little Egg Harbor. Therefore, cumulative evidence suggests that the part of the system most suitable for picoplankton in general (Olsen and Mahoney, 2001) is the area most suitable for *A. anophagefferens*. A secondary benefit of the survey is that it unquestionably promoted awareness of *A. anophagefferens* blooms in New Jersey.

Judging from 1999 *A. anophagefferens* bloom dynamics, bloom development of the species in the study region can be quite varied and complex, with multiple major pulses, short-term spatial and temporal waxing and waning, and in one instance a temporary shift in zone suitability. The multiple bloom pulses in 1999 and also during the 1997 *A. anophagefferens* bloom suggest that this may be characteristic of such blooms in the New Jersey center. Large differences in cell abundance, e.g., 100 %, were sometimes found in samples from the same general time (USEPA bay offshore helicopter supplementary sampling often was 1-2 days apart from the routine sampling) and location. This could reflect, as discussed by Lucas et al. (1999a; 1999b), such factors as higher growth rate in specific locales, population segment decline, hydrological conditions, or wind/weather conditions. Patchy spatial distribution likewise is a common feature of *A. anophagefferens* blooms in Long Island (Nuzzi and Waters, 1989).

A disconnect became apparent between A. anophagefferens bloom development in 1999 in the Barnegat Bay-Little Egg Harbor system, and in Great Bay. Blooming in the first system had earlier initiation, greater intensity, and longer persistence. Particular disconnect instances were also observed, including major population decrease in one but not the other system in May and June. Multiple reasons for the relative suitability of these two systems for A. anophagefferens likely were operative. One factor may have been the great difference in flushing between them. [Flushing has had importance in the regulation of some Long Island A. anophagefferens blooms (Nuzzi and Waters, 2004).] The annual freshwater runoff into the Barnegat Bay-Little Egg Harbor system is 2-3 times the bay volumes, but the annual runoff for the Mullica River is ~19 times the Great Bay volume, resulting in a much higher flushing rate (Durand, 1984). It is tempting to speculate that relative suitability of the systems for A. anophagefferens may also partly be due to fundamental difference in water quality. The Barnegat Bay-Little Egg Harbor system has been classified as moderately eutrophic (Seitzinger and Styles, 1999; Seitzinger, personal communication), and excessive nutrient enrichment, especially from nonpoint souces, has been implicated in the stimulation of algal growth in the system in recent years (Kennish, 1997). Great Bay, by contrast, is considered relatively pristine (Durand and Nadeau, 1972; Kennish and O'Donnell, 2002). Proportions of inorganic and organic nutrients, but not increased nutrient concentrations, were implicated in A. anophagefferens bloom development in Long Island (LaRoche et al., 1997). However, in laboratory batch culture A. anophagefferens grows best and maintains high abundance longest when amply supplied with macro- and micronutrients, and A. anophagefferens has essential micronutrient requirements including selenium, cobalt, vitamin B₁₂, and thiamine (Mahoney, 2005). We suspect that in 1999 at least A. anophagefferens bloom intensity and duration in the Barnegat Bay-Little Egg Harbor system was nutrient-associated, and that non-catastrophic MayJune bloom population declines in either system were due to nutrient insufficiency. Perhaps supporting this is that in 1999 the third bloom pulse, in the last quarter of the year, developed only in the Barnegat Bay-Little Egg Harbor system, although a seed population $(1-5 \times 10^3 \text{ cells ml}^{-1})$ persisted in Great Bay in September through November and increased to $\sim 4 \times 10^3 \text{ cells ml}^{-1}$ by late December. Assessment of the possible role of eutrophication in fostering A. anophagefferens blooms in the Barnegat Bay-Little Egg Harbor system through comparison of bloom development and chemical, physical, and associated hydrological conditions in both systems (perhaps combining chemical analyses and algal bioassay for assessment of nutrient limitation) is needed.

The concurrence of A. anophagefferens blooms in 1985 in eastern Long Island, NY, bays, Narragansett Bay, RI, and possibly Barnegat Bay, NJ, led to the hypothesis that regional climatological and/or hydrographical events were operative in their regulation (Smayda and Villareal, 1989; Cosper et al., 1989). A. anophagefferens either did not bloom in the Barnegat Bay-Little Egg Harbor system and Great Bay from 1989 through 1994, or its blooms were of low intensity and went unnoticed or unreported. What may have restricted blooming of the species in New Jersey during these years is unknown. Suggesting some kind of regulation encompassing both sides of the Bight in this period, A. anophagefferens blooms did not occur in the Long Island Peconic Bay system or eastern south shore bays in 1989, 1990, and 1993, and occurrence was limited to low intensity blooms (<2.5 x 10⁵ cells ml⁻¹) in one or both Long Island systems in 1991, 1992, and 1994. Moreover, overall Long Island bloom incidence was greater in 1995 through 2001 (Nuzzi and Waters, 2004; Nuzzi, personal communication). Great Bay water temperature and salinity levels in March through June 1985-1990 (Able et al., 1992) do not suggest A. anophagefferens regulation by these factors in this bay. Because the 1985 A. anophagefferens blooms developed in particular bays but were absent in contiguous or relatively nearby waters, Smayda and Villareal (1989) also postulated a second-level regulation mediated by local events. Second-level A. anophagefferens regulation has had importance, at times, in New York Bight coastal bays since then. Wide distribution and relatively high abundance of A. anophagefferens in 1999 in southern New Jersey estuarine waters between Great Bay and Cape May (Mahoney et al., 2003b), coincident with the major bloom of the species in the Barnegat Bay-Little Egg Harbor system and Great Bay described in this report, suggests prevalence of bloom-favorable conditions throughout the entire New Jersey coast during April through June. If so, bloom-promoting conditions in the New York Bight apparently were restricted to the western side. The species did not bloom in the Long Island Peconic Bay system in 1999, and bloom development in Great South Bay was unusual in that A. anophagefferens was undetected until September, when a bloom initiated which developed into December (Nuzzi and Waters, 2004). The time period of the Great South Bay bloom approximated that of the third, and least intense, bloom pulse in the Barnegat Bay-Little Egg Harbor system.

Formation and duration of Long Island *A. anophagefferens* blooms have been influenced by salinity and water temperature (Nuzzi and Waters, 2004), and these factors likewise at times had second-level regulatory importance in the 1990s New Jersey *A. anophagefferens* blooms. During our survey salinity had greatest second level regulatory importance. *A. anophagefferens* has considerable ability to adapt to relatively low salinity (e.g., 21-22 PSU), but grows best with higher salinity (Cosper et al., 1989; Mahoney, 2005); its blooms in eastern Long Island characteristically developed with salinities ≥27 PSU (Bricelj and Lonsdale, 1997). In 1998 and 1999, mean salinity levels in the Barnegat Bay-Little Egg Harbor system consistently were

highest in the southern zone and lowest in the northern zone; central zone salinity was closest to southern zone salinity. Therefore, it is expected that the southern and central zones would be most favorable for A. anophgefferens bloom development. Salinity change in the three zones in the respective years generally was linked with respect to time and prevailing direction of change (Figs. 25, 26). Salinity level and pattern of change in the two years differed greatly. January salinity levels were relatively high in 1998; with the exception of a temporary increase in April, salinity decrease progressed from February through May, when annual low levels were reached. In 1999, January salinity levels were the lowest for the year; relatively high levels were present in February and subsequently salinity increased moderately, or was little changed, through April. In both years, beginning in May or June, salinity progressively increased through mid-August. In 1998, salinity levels varied little or continued to increase moderately, depending on the zone, for the remainder of the year. In 1999, salinity levels decreased through October, especially in the northern zone. Also indicative of contrasting salinity conditions in the system during these years is that difference between northern and southern zones mean salinity levels, annually and during the March-June pre-bloom and bloom initiation/development periods, was ~9-10 PSU in 1998, but only ~6 PSU in 1999.

Salinity conditions in the Barnegat Bay-Little Egg Harbor system in much of the first half of 1998 apparently prevented bloom development. The New Jersey coast experienced approximately weekly storms from mid-January through March; precipitation was ~18 cm above normal for the period January through March (calculated from 1998 U. S. National Weather Service data for Atlantic City, New Jersey) which greatly lowered salinity. Even if *A. anophagefferens* had adapted to lower salinity during February-March, salinity in the southern and central zones was just above the lower limit for suitability in the second half of April, and decreased to marginal or lower levels in May (when *A. anophagefferens* bloom development would be expected). Mid-May mean salinities were 11.5, 20.5, and 20.1 PSU, respectively, in the northern, central, and southern zones of the survey region, respectively (Fig. 25). Mean salinity increased to ~25 PSU in June, and to ~27 PSU in July in the southern zone, when slightly lower salinities (~24-26 PSU) were present in central Barnegat Bay. Much lower salinities prevailed in northern Barnegat Bay through the summer and did not increase to even marginally favorable levels until September.

In 1999, salinity conditions (Fig. 26) in March through June doubtless favored *A. anophagefferens* bloom formation. Salinity during this time in the southern zone (including the bloom primary locus) was ≥26 PSU (~7 PSU higher than in 1998). Salinity increased to ≥26 PSU in the central zone approximately in mid-May, and in the northern zone in early July. Salinity level and bloom development in the various zones appear associated. Constancy of a range of salinities optimal for bloom development (~26-30 PSU) in the southern zone in March-June provides a basis for comparison. *A. anophagefferens* blooming initiated in late April-early May in this zone (specifically in southern Barnegat Bay and adjacent Little Egg Harbor), and bloom development was well underway by mid-May. Then *A. anophagefferens* blooming initiated in the central zone in the first week of June, coincident with salinity increase in the zone to ≥26 PSU. A lower but considerable population (2-4 x 10⁵ cells ml⁻¹) which persisted for at least two weeks was reached in the lower northern zone in mid-June, coinciding with a salinity rise from ~22 PSU to ~24 PSU. With little change in salinity levels, the bloom continued in all zones until it collapsed in early July.

Despite a system-wide salinity decrease in 1999 from mid-August through the second half of October, as much as ~6 PSU in the southern and central zones and ~9 PSU in the northern zone, salinity levels in the southern and central zones remained \geq 26 PSU. This likely favored initiation of the third bloom pulse in September in the bloom primary locus, and subsequent bloom development in October and November in the central zone. Especially pronounced salinity decrease in the northern zone, which began in mid-September and persisted through December, resulted in salinity levels \leq 23 PSU, either marginal or unfavorable for bloom development, through the remainder of the year. Even when temperature and salinity were suitable in the northern part of the northern zone (sites 46, 49), *A. anophagefferens* did not bloom there, suggesting other regulatory factor(s) were operative -- although modest cell abundances of 3-4 x 10^3 cells ml $^{-1}$ were found in October and November.

Comparison of 1998 and 1999 seasonal water temperatures (Figs. 27, 28) in the expected period of bloom initiation and development, April through June, does not suggest a temperature basis for occurrence of an *A. anophagefferens* bloom in one year and bloom absence in the other. Throughout 1998 and 1999, respectively, seasonal change of water temperature in the southern, central and northern zones of the Barnegat Bay-Little Egg Harbor system basically was linked. Water temperature, unlike salinity, did not mediate zone-to-zone suitability for *A. anophagefferens* growth. Minor year-to-year differences include ~2 °C warmer water temperature in 1998 than in 1999 from late April through May. (Water temperatures during this period in both years were <25°C, so were suitable for *A. anophagefferens*.) In the first half of June, 1999 water temperature was 2-6°C warmer than 1998; water temperature difference between these years in the second half of June was <1°C.

In 1999, temperatures $\geq 12^{\circ}\text{C}$ - $\leq 25^{\circ}\text{C}$ -- a range favorable to growth of A. anophagefferens (Cosper et al., 1989) -- were present from early April to the third week of June (Fig. 28). Comparison of A. anophagefferens cell abundance with water temperature in various locales of the study region southern and central zones shows that highest abundances primarily were associated with water temperatures in the range $18-22^{\circ}\text{C}$. The bloom population persisted through a temperature increase to $25-26^{\circ}\text{C}$ of approximately a week duration (in the second week of June), and greatest cell abundance followed this, associated with temperature decrease to $\sim 22^{\circ}\text{C}$. The bloom declined dramatically in the Barnegat Bay-Little Egg Harbor system in the last week of June, although there was little change in temperature, suggesting regulation by another factor. Following the onset of water temperatures $\geq 29^{\circ}\text{C}$ in the first week of July, unfavorably high temperatures ($27-29^{\circ}\text{C}$) prevailed until the third week of August, although with short term (<one week) decreases to the $22-26^{\circ}\text{C}$ range, and the population remained in low abundance (primarily $\leq 10^3$ cells ml⁻¹). Temperature became consistently favorable again in the last week of August throughout the study region, permitting third bloom pulse development.

Absence of *A. anophagefferens* bloom development in June, 1998 is not explained by regulation associated with either water temperature or salinity then present. Water temperature did not become unfavorable (>25°C) for *A. anophagefferens* until late June (Fig. 27), and salinity became at least moderately favorable in southern and central zones earlier in the month (Fig. 25). General pico-nanoplankton population abundance in the study area was reached in May and continued through August; levels of the chlorophyte *N. atomus* alone were >10⁵ cells ml⁻¹ in May and June, and were >5 x 10^5 cells ml⁻¹ in July-August (Olsen and Mahoney, 2001). Suppression of *A. anophagefferens* bloom development by competition from various other piconanoplankton spp. may have been a factor. However, conditions in the southern zone generally

less favorable for pico-nanoplankton spp. may have been operative because southern Barnegat Bay mean chlorophyll level and maximum abundance of these forms were the lowest for the entire 11-year NJDEP survey (Olsen and Mahoney, 2001).

Prevailing Secchi depths of ~ 0.3 -0.4 m in the bloom primary locus during an A. anophagefferens abundance peak in the third week of June 1999 (the lowest values found in the survey) suggests the possibility of light limitation at times through attenuation by the population. [Light availability is a potentially important factor in Long Island A. anophagefferens blooms (Milligan and Cosper, 1997).] Also suggesting light regulation of some phytoplankton in the study region, benthic microalgal production rates in northern Barnegat Bay were highest when bottom light was $>50 \mu E \text{ m}^{-1} \text{ S}^{-1}$, and were low when bottom light was $<20 \mu E \text{ m}^{-1} \text{ S}^{-1}$ (Seitzinger et al., 2001). However, A. anophagefferens would be expected to flourish under low irradiance conditions because its utilization of light is highly efficient; this may be complemented by heterotrophic ability (Milligan and Cosper, 1997). Field observations of healthy cells at 20 m depth during a major Long Island bloom, where light likely was very low, and on another occasion recovery of healthy cells from beneath considerable ice cover (Nuzzi and Waters, 1989, 2004), support perception that A. anophagefferens has wide physiological flexibility in this regard. Nuzzi and Waters (1989) speculated that, because of the apparent constancy of macronutrient concentrations in Long Island bloom waters, micronutrients -- particularly trace metals or trace organics -- may have an important regulatory role. Bioassays of A. anophagefferens growth in water from Long Island bays where its blooms were or were not occurring suggested regulation at times by iron and selenium (Cosper et al., 1993). Apart from regulation which permits or prevents an A. anophagefferens bloom, the 1999 New Jersey bloom history shows that a bloom, when underway, can be temporarily regulated by a transitory factor. Perhaps an important temporary regulator is availability of one or more macronutrients or micronutrients, especially when competition for these from other pico-nanoplankton is intense.

Comparison of the 1995, 1997, and 1999 New Jersey *A. anophagefferens* bloom development with that of well-studied Long Island occurrences suggests some differences may be characteristic. *A. anophagefferens* bloom initiation and development may be earlier in the year in the Barnegat Bay-Little Egg Harbor system than in eastern Long Island. The 1995 and 1997 New Jersey blooms possibly initiated in the second half of April and the first half of March, respectively; it is certain that the 1999 bloom initiated in late April-early May. Long Island blooms typically initiated in late May (Bricelj and Lonsdale, 1997). Peak intensity of the 1995 New Jersey bloom possibly was in May or early June; peak of the 1997 New Jersey bloom was in April. This was earlier than Long Island blooms, which typically attained peak abundance in June or July (Bricelj and Lonsdale, 1997). The 1999 New Jersey bloom was similar to typical Long Island blooms in attainment of peak abundance in June, although abundances rivaling those of Long Island bloom maxima had been reached by late May-early June.

Salinity apparently can have greater variation spatially or temporally, and more importance in the regulation of *A. anophagefferens* blooms, in the Barnegat Bay-Little Egg Harbor system, than in Long Island bloom loci. In 1998, salinities \leq 23 PSU, completely unsuitable for *A. anophagefferens* growth or requiring long adaptation, predominated in the New Jersey study region from January through May, encompassing pre-bloom and bloom development periods. Salinity of eastern Long Island *A. anophagefferens* bloom loci rarely falls below levels favorable for growth of the picoplankter, which negates it being a primary regulator of its blooms there (LaRoche et al., 1997). Thermal regulation of *A. anophagefferens* blooms

may occur with greater frequency in New Jersey than in Long Island. Thermal regulation of a Long Island *A. anophagefferens* bloom occurred in July 2000 (Nuzzi and Waters, 2004), but typically Long Island blooms do not wane until late summer (Bricelj and Lonsdale, 1997). It is likely that thermal regulation truncated all three 1990s New Jersey *A. anophagefferens* blooms. Water temperature apparently permitted endurance of moderate *A. anophagefferens* bloom populations in the Barnegat Bay-Little Egg Harbor system into July of 1995 and 1997, but not through summer. When the 1995 bloom collapsed is uncertain but likely this was in the second half of July. In 1997, bloom collapse was complete by the end of July, presumably with the whole system reaching its typical ~28°C peak summer temperature (specific data are lacking). Sudden, complete bloom collapse was associated with high water temperatures (≥ 29 °C) throughout our study region in the first week of July, 1999.

Maximum intensities of the 1990s A. anophagefferens New Jersey blooms appear to at least rival the intensities of the Long Island blooms. Enumerations of the 1985 Long Island A. anophagefferens blooms by light microscopy (which may have included morphologically similar picoplankton) provided population estimates of <3 x 10⁶ cells ml⁻¹ in Great South Bay, and 2 x 10⁶ cells ml⁻¹ in Flanders Bay; the latter bay was reported to have had the highest abundance in the Peconic estuary system (>2.5 x 10⁶ cells ml⁻¹ in 1986); cell abundances of annual blooms diminished through 1988 (Nuzzi and Waters, 1989, 2004). From 1988 through 1995, A. anophagefferens blooms in various Long Island bays, with enumerations by the much more reliable immunofluorescence method (SCDHS data reported in Bricelj and Lonsdale, 1997), had maxima at times of $< 2 \times 10^6$ cells ml⁻¹. In mid-April 1997, the bloom in New Jersey achieved an abundance of $\sim 4 \times 10^6$ cells ml⁻¹ in Little Egg Harbor, considerably in excess of reported Long Island maxima. Because of especially limited spatial sampling, whether this level represents general bloom development or passive concentration in a limited area was not confirmed. However, supporting suspicion that the April 1997 levels represented general A. anophagefferens population growth, and as an additional example of high intensity of New Jersey blooms, the same maximum population level was obtained again in southern Barnegat Bay and eastern Little Egg Harbor in 1999, accompanied by levels of 1-3 x 10⁶ cells ml⁻¹ in adjacent areas. The typical two- or three-month duration of Long Island A. anophagefferens blooms (Bricelj and Lonsdale, 1997) is rivaled by the New Jersey blooms.

Physical characteristics of bays most suitable for *A. anophagefferens* bloom development on the western side of the New York Bight basically are similar to those of bloom loci on the eastern side. Incidence of eastern Long Island *A. anophagefferens* blooms is restricted to shallow, relatively unstratified estuaries having limited flushing (Bricelj and Lonsdale, 1997), which description certainly fits the Barnegat Bay-Little Egg Harbor estuarine system. Great Bay has some of these characteristics but is relatively well flushed. Also noteworthy is that both New Jersey and New York bloom centers are at considerable distance from the inner New York Bight or Apex. *A. anophagefferens* has had wide distribution and long term presence in New York Bight Apex waters, such as the Hudson-Raritan estuary, Jamaica Bay, and South Oyster Bay (Mahoney et al., 2003b), but it has not bloomed anywhere in the Apex. In generally bloomprone Apex waters, including Sandy Hook Bay and Jamaica Bay, does inadequate level of an essential nutrient or presence of inhibitory substances restrict *A. anophagefferens* growth?

SUMMARY, CONCLUSIONS, AND QUESTIONS

Three major *A. anophagefferens* blooms in the Barnegat Bay-Little Egg Harbor system and contiguous Great Bay in the 1990s identified these bays as a major bloom center. Little Egg Harbor and southern Barnegat Bay in the southern zone constituted the primary initiation and development locus of the 1999 bloom, and Little Egg Harbor was part or all of the development locus for the three bloom pulses in 1997. The southern zone, which is the part of the system most suitable for picoplankton in general, is the area most suitable for *A. anophagefferens*. Bloom development during the fall pulse in 1999 shifted to the central zone, showing that an alternate bloom locus can emerge under certain circumstances. Based on the suitability of the study region and *A. anophagefferens* distribution studies from Great Bay south to Cape May (Mahoney et al., 2003b), we consider a similar complex of bays or "sounds" connected by intracoastal channels (including the Intracoastal Waterway) along the New Jersey coast likely to be additional loci for future blooms.

In 1998-1999, during winter and when conditions were detrimental in summer, the *A. anophagefferens* population in the study region decreased to low levels (at times and certain places below level of detection), but always remained detectable in some locales. What percentage of a growth season population survives to provide seed population for the next growth season is unknown. Sampling in the surveys was only in the upper meter. Difference in population abundance between surface and bottom, e.g., along the track of the Intracoastal Waterway, remains undetermined.

The 1999 *A. anophagefferens* bloom had a series of pulses; individual pulses were complex, having varied spatial and temporal intensity. How typical the 1999 bloom is of *A. anophagefferens* blooms in the study region is undetermined. The 1997 *A. anophagefferens* bloom likewise had had multiple pulses, however. This feature may be characteristic of such blooms in the study region.

A bloom regulation disconnect, at least at times, between the Barnegat Bay-Little Egg Harbor system and Great Bay appears probable -- e.g., the late June decline in the bloom primary locus, but no coincident bloom decline in Great Bay. The eutrophication of the Barnegat Bay-Little Egg Harbor system versus the relatively pristine state of Great Bay, and the much greater flushing of Great Bay, are obvious contrasts between the two systems. An *A. anophagefferens* bloom in a specific locale of the study region apparently may be temporarily limited. The possibilities of such limitation by macro- or micronutrients or light remain to be assessed.

Conditions along the New Jersey coast in April through June of 1999 were highly favorable to *A. anophagefferens* growth in general, and its bloom development in certain areas. Although this was restricted to the western side of the New York Bight, it brings to mind the suggestion by Smayda and Villareal (1989) and Cosper et al. (1989) that regional climatological and/or hydrographical events could have been operative in development of the 1985 blooms. Second level regulation of bloom development in the New Jersey study region in 1998-1999 by salinity and temperature had clear importance. Of these, salinity was the most important. We conclude that unfavorably low salinity in much of the first half of 1998 prevented bloom development. Temperature had the lesser but important effect of truncating the 1999 bloom.

A possible implication of *A. anophagefferens* intolerance to low salinity is that if the species is subjected to marginal or unsuitably low salinities when it would otherwise initiate bloom growth (e.g., during extra-strong spring freshening), it will not grow optimally or at all for

a time. If this lag period is sufficiently long it may lose its "window of opportunity" through delay of potential for optimum growth to when water temperature in the Barnegat Bay-Little Egg Harbor system is unfavorably high, or when competitor pico-nanoplankton spp. typically bloom. *A. anophagefferens* has flourishing growth when water temperature is ~20°C (Cosper et al., 1989), but this is shared with the general pico-nanoplankton assemblage it has to compete with (Olsen and Mahoney, 2001). It is therefore likely that one of the main determinant factors in its bloom development is ability to grow at low water temperatures (Cosper et al., 1989), long before competitor pico-nanoplankters are favored. Unquestionable disadvantage to *A. anophagefferens* is the higher temperature tolerance of at least some competing pico-nanoplankton, including the typically dominant *N. atomus*. We speculate that if *A. anophagefferens* grows to abundance prior to when conditions permit rapid growth of its competitors, then barring inimical physical conditions a relatively high population of the species may co-exist with the assemblage developing later; but if competitors gain ascendancy in advance of *A. anophagefferens* it can subsist only as a sub-dominant or minor phytoplankton assemblage constituent.

Differences in time of initiation, time of maximum intensity and termination may be characteristic of the New Jersey and Long Island *A. anophagefferens* blooms, with New Jersey earlier in the year than Long Island. Second level regulation by salinity and temperature may have greater importance in the New Jersey center than in eastern Long Island bays. Maximum intensity of the blooms in our study region at least rivals that in Long Island; the typical duration span is comparable in both centers.

Effects of the 1995, 1997, and 1999 New Jersey *A. anophagefferens* blooms on natural flora and fauna were not determined. The detrimental effects of each bloom on hard clam, *M. mercenaria* -- including growth inhibition of juveniles -- in a Little Egg Harbor aquaculture facility is evidence of consistently toxic nature. Bricelj and Lonsdale (1997) emphasized that *A. anophagefferens* blooms in Long Island bays, typically occurring in June-July, coincide with the spawning period, planktonic larval development, and juvenile growth of several commercially important bivalves. Effects of the 1995, 1997, and 1999 New Jersey blooms on cultured hard clam may have been influenced similarly by timing of the aquaculture operation. High mortality of cultured clam larvae was associated with the 1995 bloom; feeding inhibition and growth cessation in juvenile clams over 6-8 week periods was experienced during the 1997 and 1999 blooms. Information on 1997 and 1999 blooms reveals that bloom initiation time can vary. This might have implications regarding *A. anophagefferens* bloom effects in the study region, e.g., whether or not *A. anophagefferens* blooms are coincident with critical stages of susceptible bivalve larval and juvenile development.

A. anophagefferens blooms ceased to have major occurrence in eastern Long Island after 2001. The Long Island blooms, for a time at least, apparently have "run their course". No certain explanation for this is at hand. How long into the future the species' blooms will continue to occur in the New Jersey center remains to be seen. The foremost suitability of Little Egg Harbor and southern Barnegat Bay for A. anophagefferens blooms in the 1990s likely is explained by this region having the foremost suitability in the region for pico-nanoplankton in general. (Pico-nanoplankton blooms there being the most widespread, and have the earliest initiation and the longest duration with sustained high cell densities.) Whether or not eutrophication of Barnegat Bay and Little Egg Harbor has importance in promoting A. anophagefferens blooms in the system remains to be determined. Higher and more consistent

salinity in the southern zone, relative to central and northern zones, likely is an important factor in this zone being the portion of the system most favorable for blooms of *A. anophagefferens*.

ACKNOWLEDGMENTS

R. Nuzzi and other staff members, particularly John Bredemeyer, Bureau of Marine Resources, Suffolk County, New York, Department of Health Services, contributed ongoing advice and cooperation, all of the enumerations for the 1995 New Jersey *A. anophagefferens* bloom, and most enumerations for the 1997 bloom. D. Anderson and D. Kulis, Woods Hole Oceanographic Institution, provided advice on immunofluorescence enumeration of *A. anophagefferens* and the primary antibody. We thank members of the USEPA, Region II, Surveillance and Monitoring Branch, particularly R. Braun and H. Grebe, for critical bay offshore water sample collections by helicopter over the course of our studies. J. Brooks, K. Wendling, and J. O. Mahoney provided technical assistance; A. Kalbach and T. Finneran provided the figure preparation; and C. Zetlin did the GIS generation of the study region base map, all NMFS, James J. Howard Marine Sciences Laboratory. We thank G. Wikfors, NMFS, Milford Laboratory, for reviewing this report, and L. Garner, NMFS, Woods Hole Laboratory, for editing the manuscript. The senior author thanks R. Robohm, NMFS, Milford Laboratory, for effective supervisory support during a critical phase of the study.

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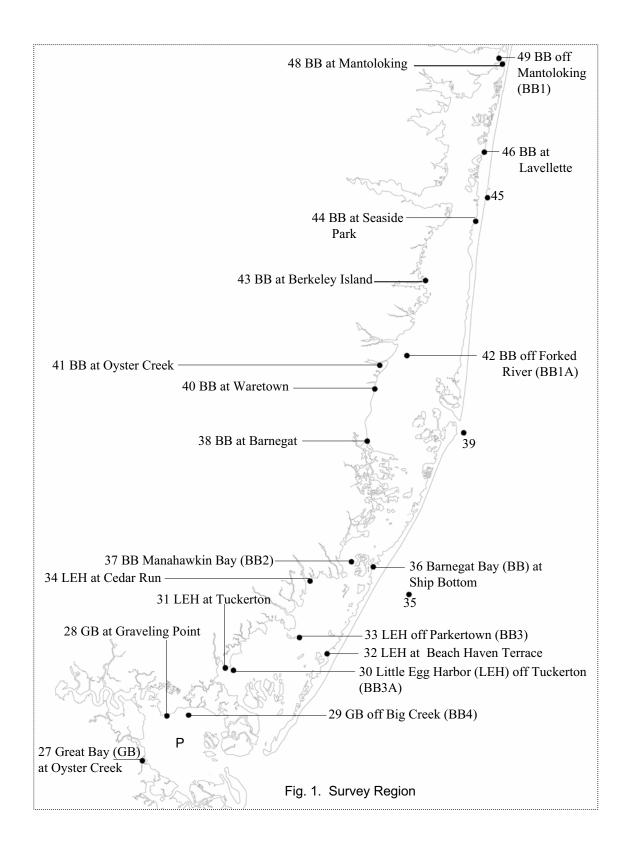


Figure 1. Map of Barnegat Bay-Little Egg Harbor system and Great Bay study region showing locations of sampling sites.

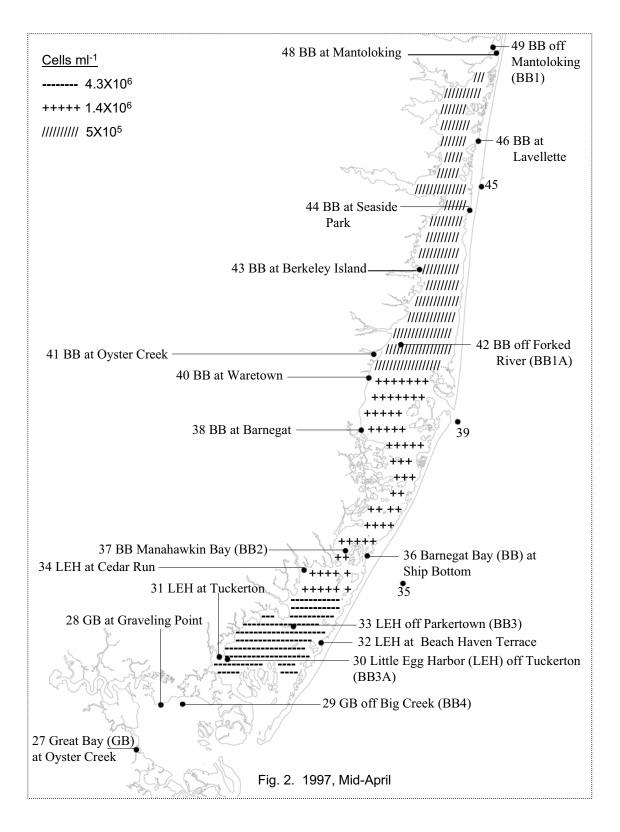


Figure 2. Bloom distribution in mid-April, 1997.

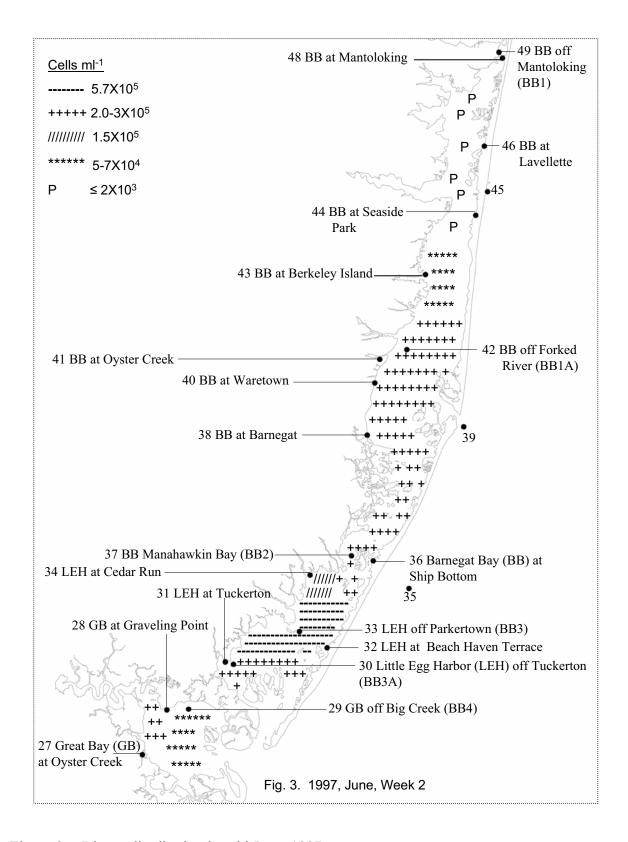


Figure 3. Bloom distribution in mid June, 1997

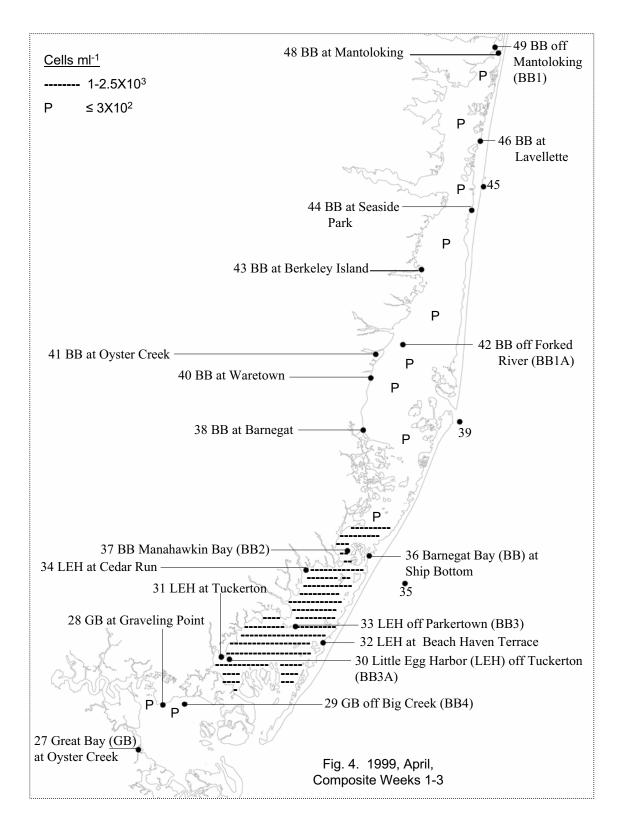


Figure 4. A. anophagefferens distribution and abundance in early to mid-April, 1999.

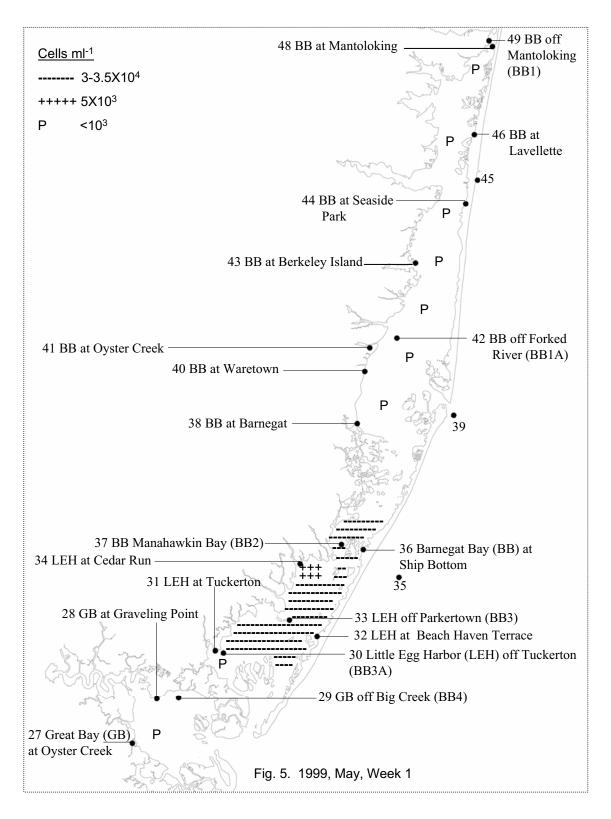


Figure 5. Bloom development in early May, 1999.

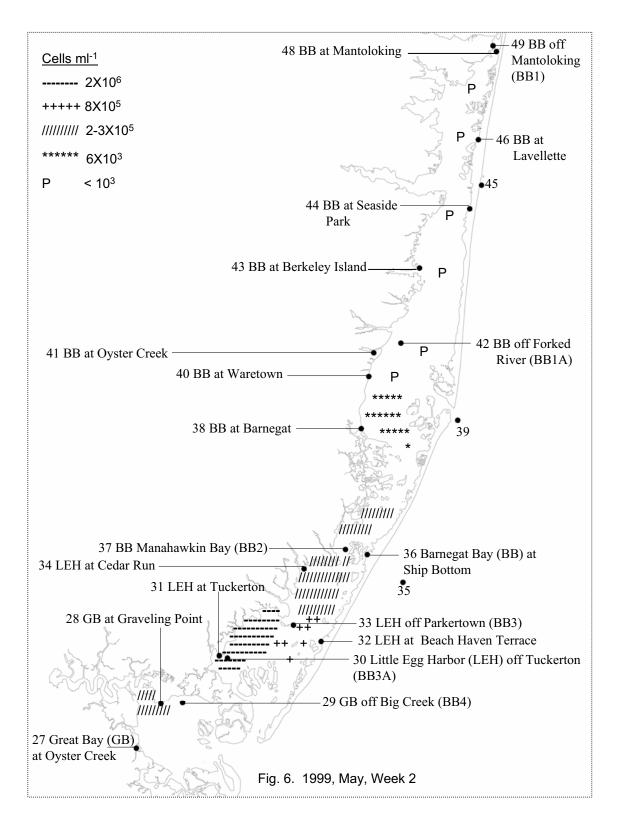


Figure 6. Bloom development in mid-May, 1999.

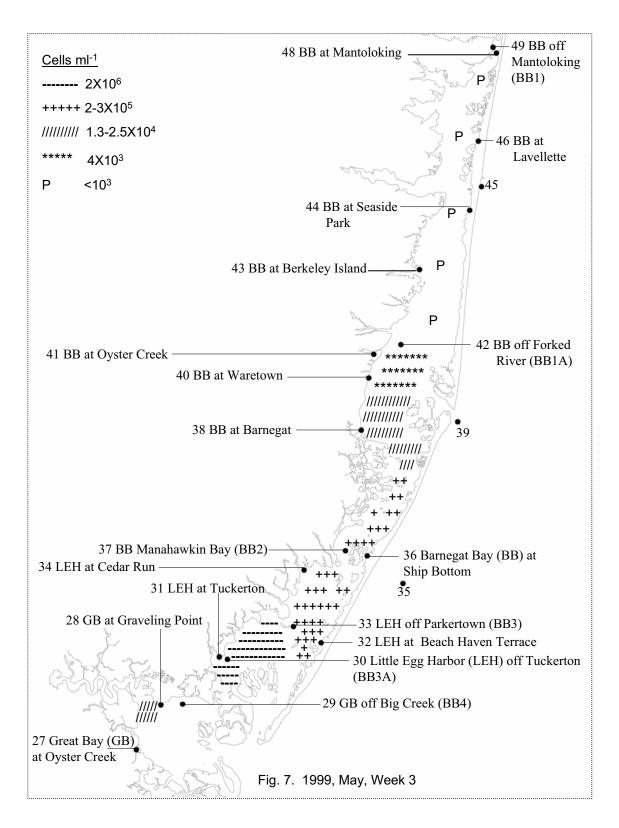


Figure 7. Bloom development in the third week of May, 1999.

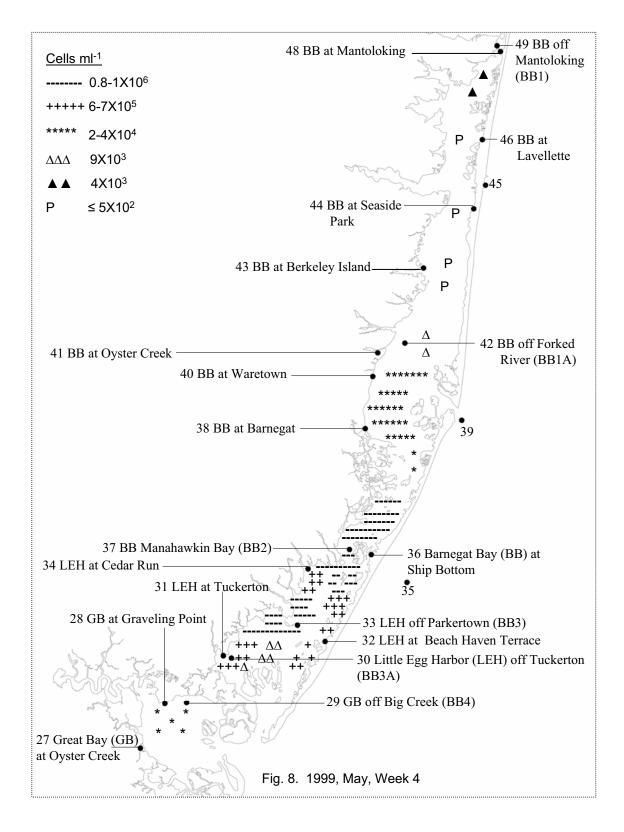


Figure 8. Bloom development in late-May, 1999.

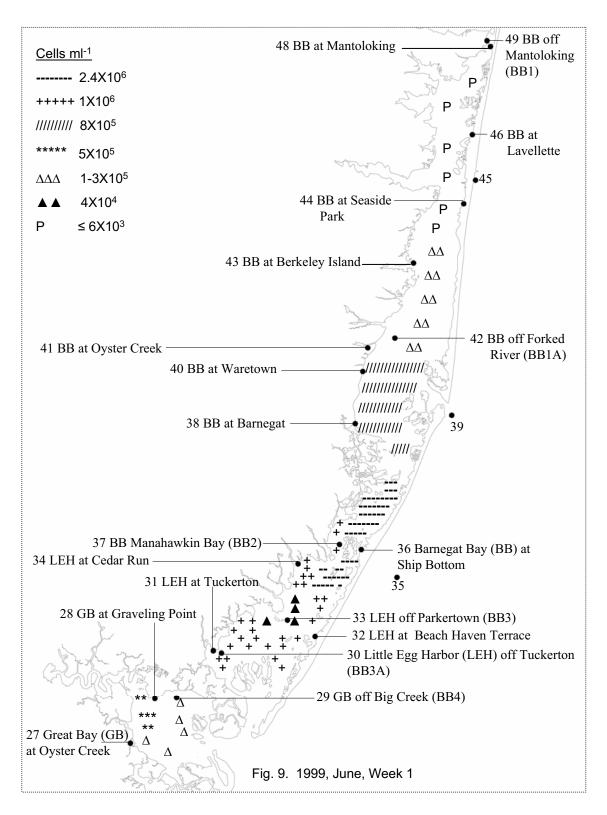


Figure 9. Bloom development in early June, 1999.

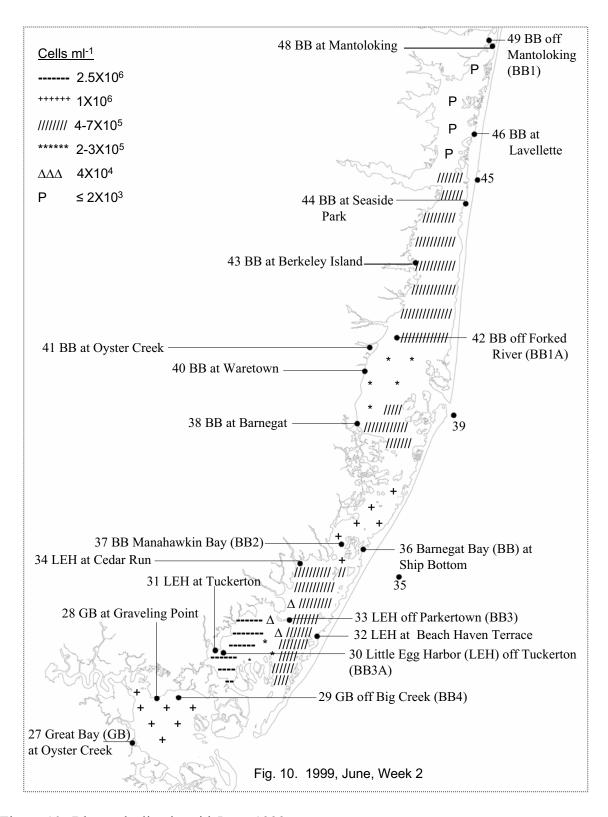


Figure 10. Bloom decline in mid-June, 1999.

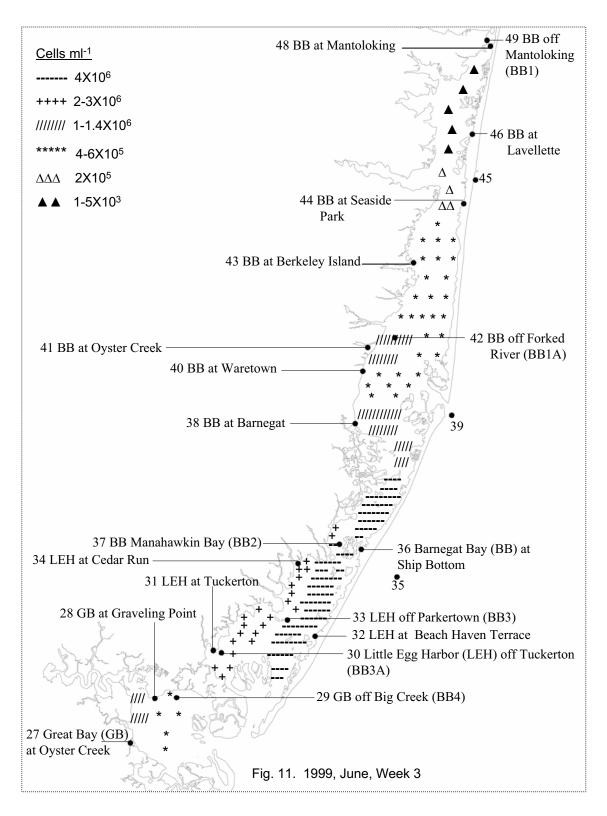


Figure 11. Second bloom pulse development in the third week of June, 1999.

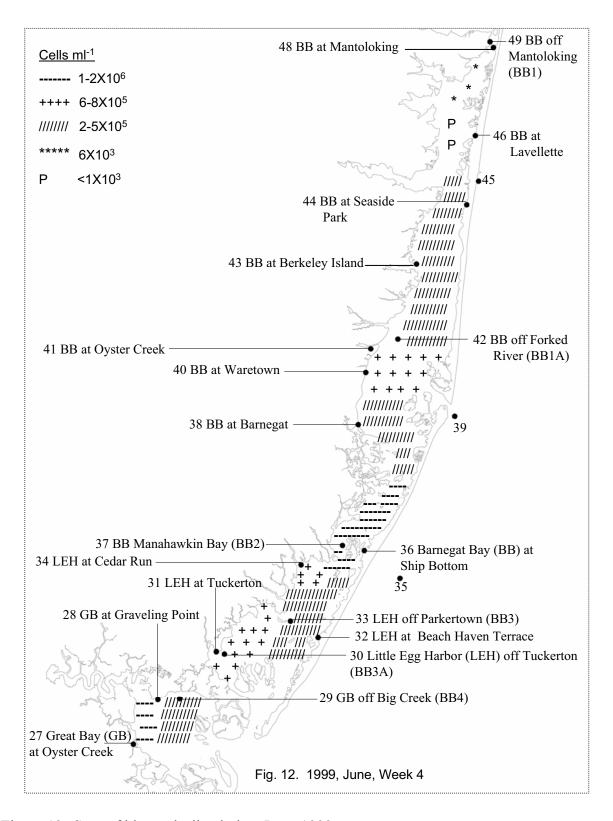


Figure 12. Start of bloom decline in late June, 1999.

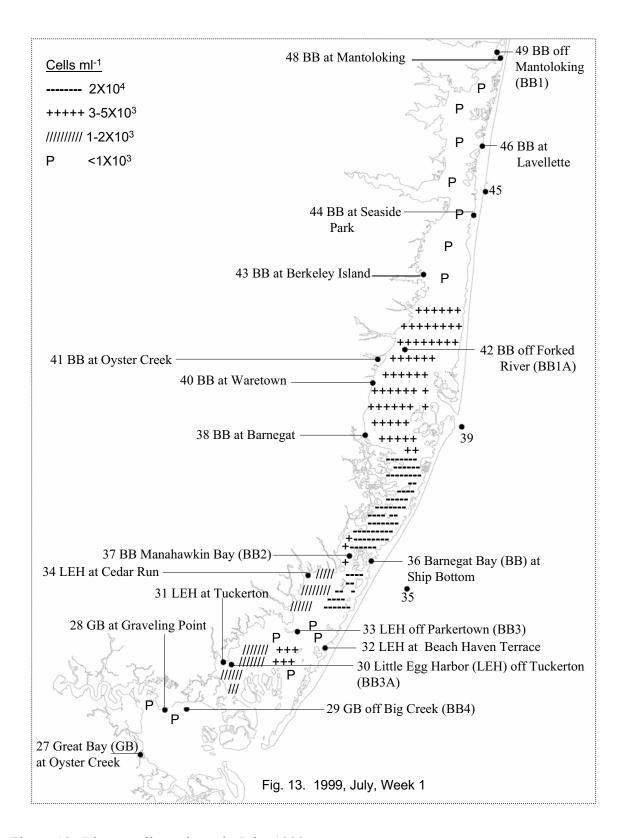


Figure 13. Bloom collapse in early July, 1999.

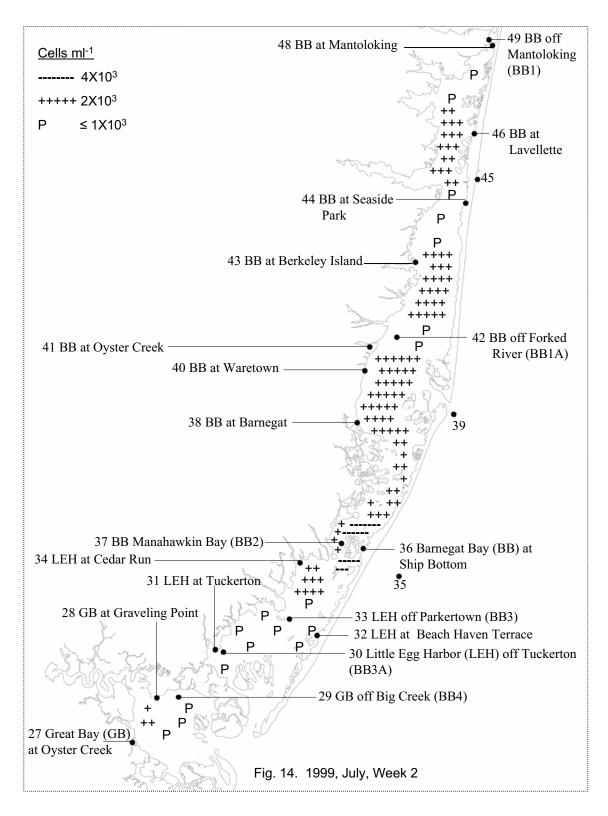


Figure 14. Continued population decrease in mid-July, 1999.

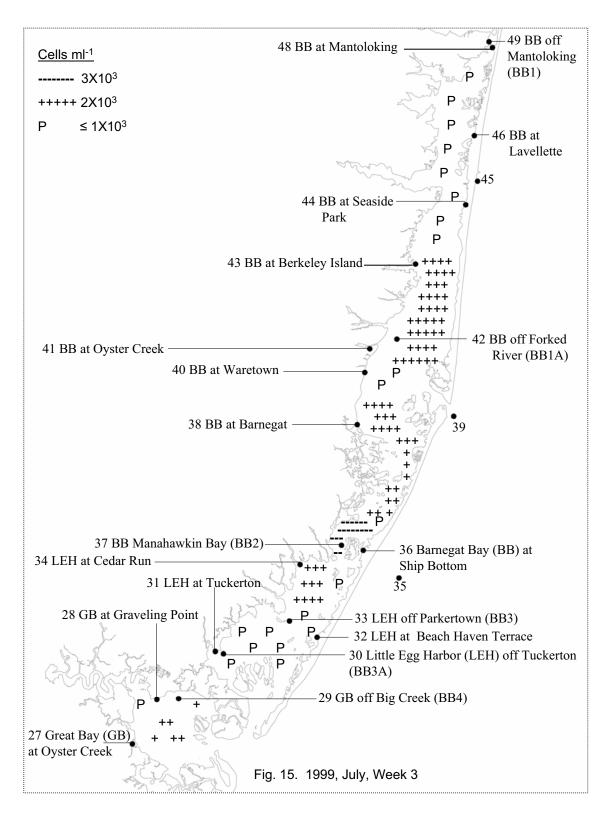


Figure 15. Population wane in the third week of July, 1999.

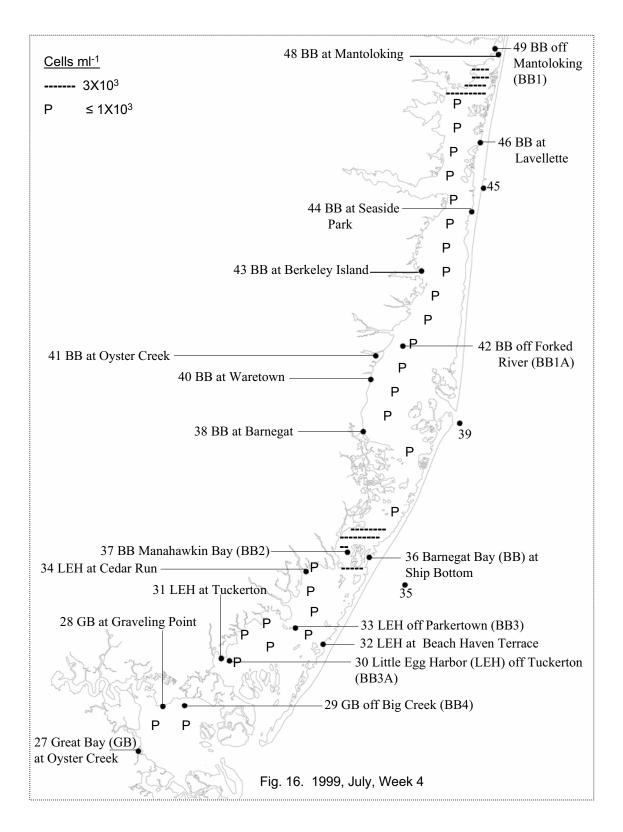


Figure 16. Further general population waning in late July, 1999.

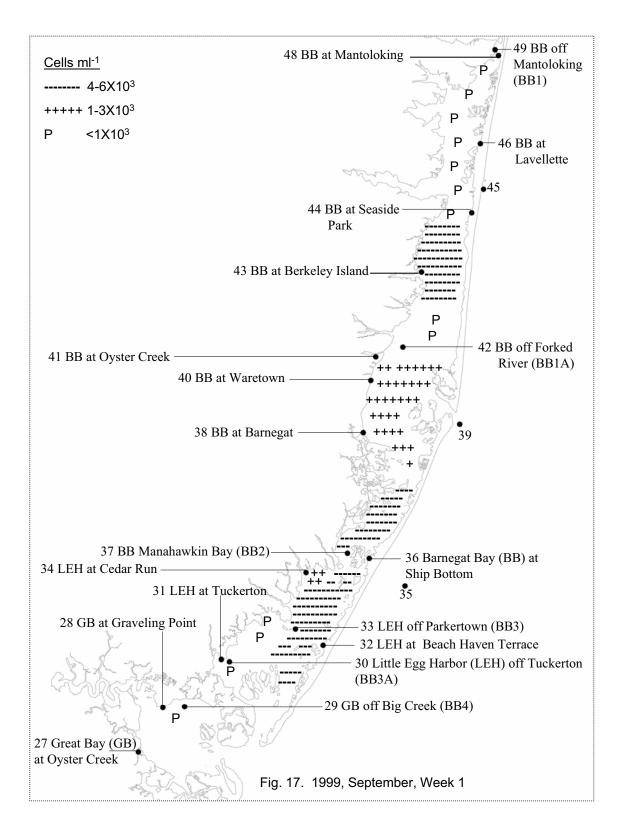


Figure 17. Third bloom pulse initiation in early September, 1999.

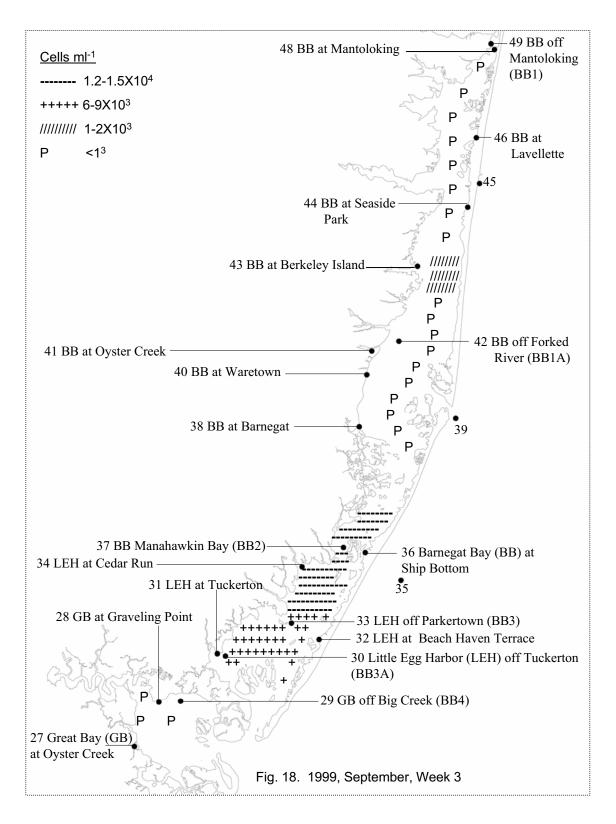


Figure 18. Bloom development in late September, 1999.

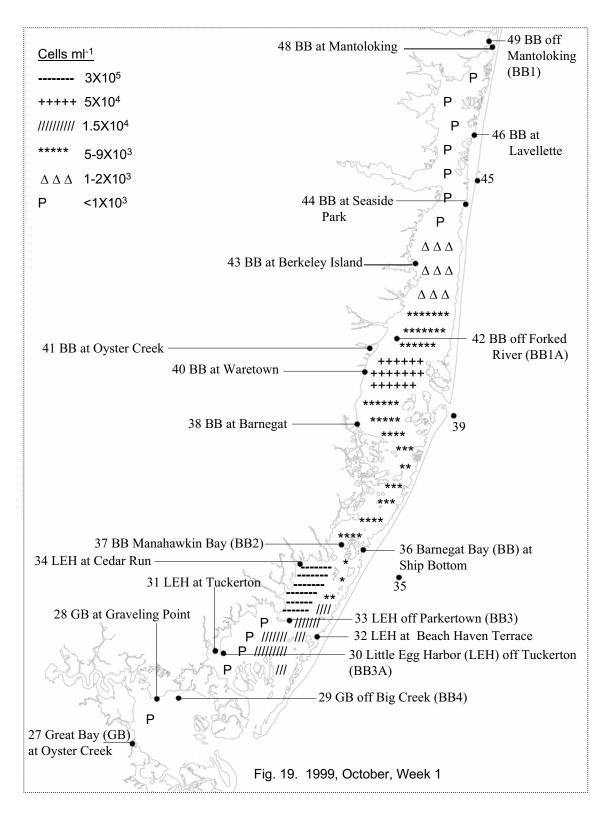


Figure 19. Bloom development in early October, 1999.

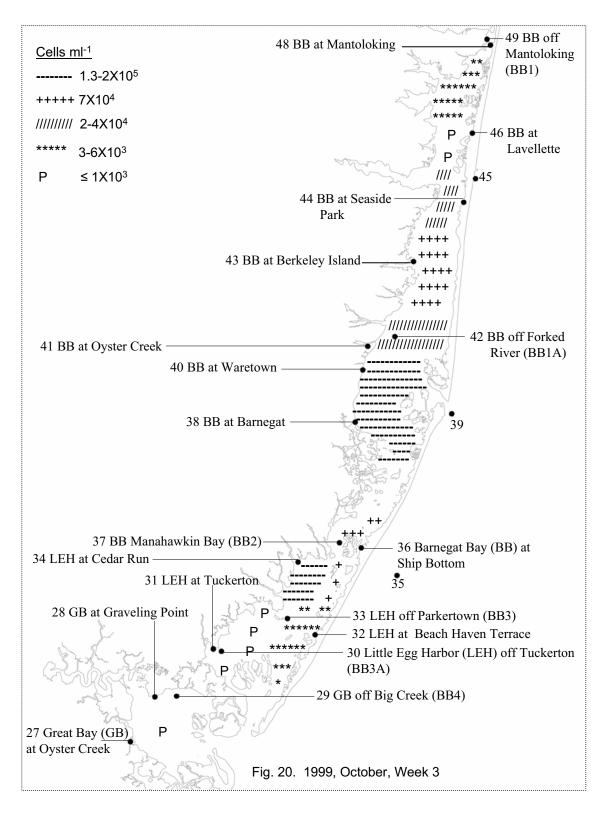


Figure 20. Bloom development in late-October, 1999.

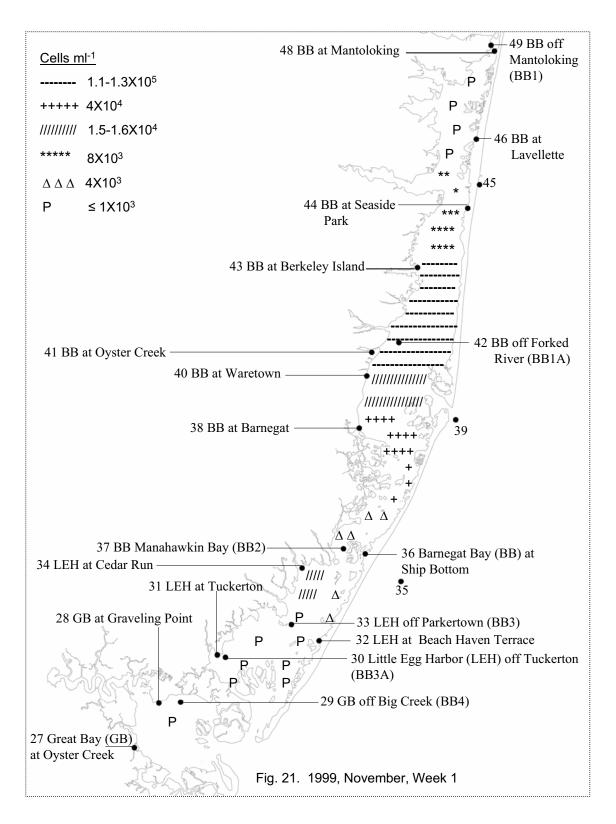


Figure 21. Bloom development in early November, 1999.

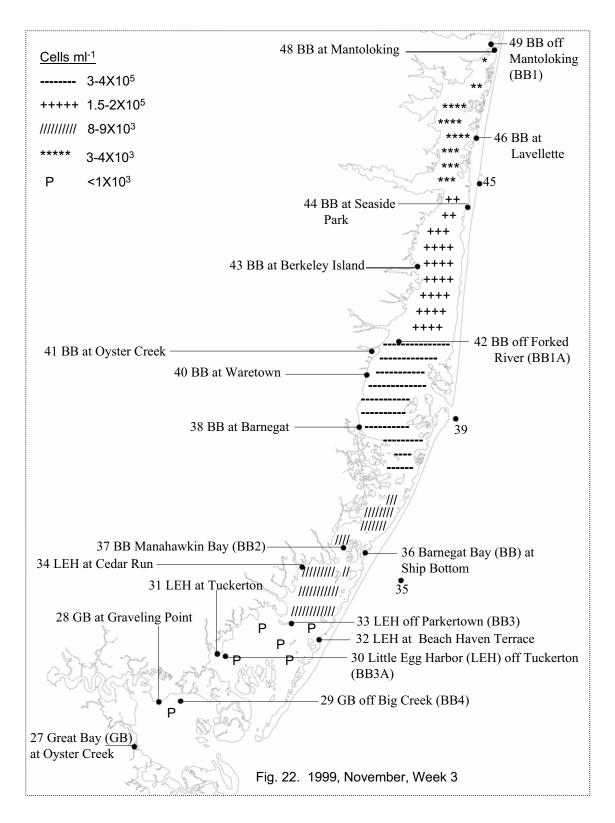


Figure 22. Bloom development in late-November, 1999.

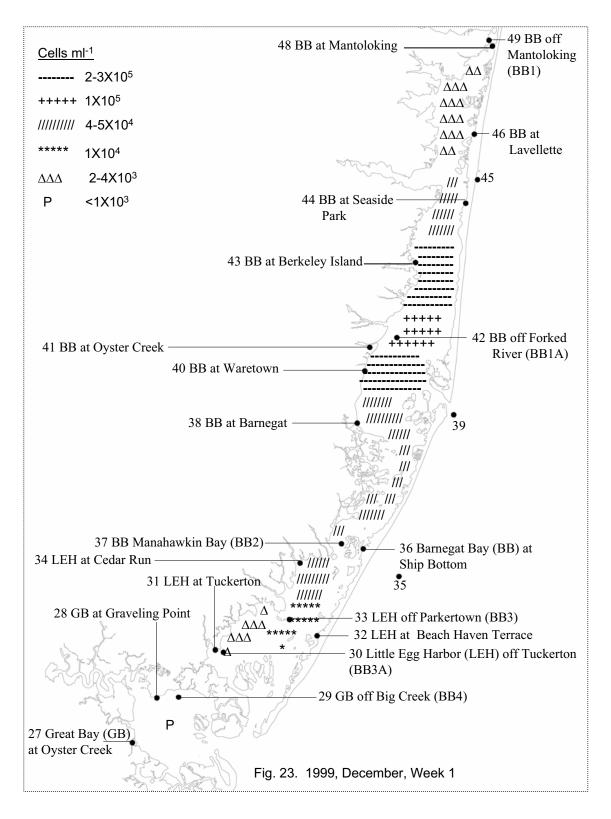


Figure 23. Bloom development in early December, 1999.

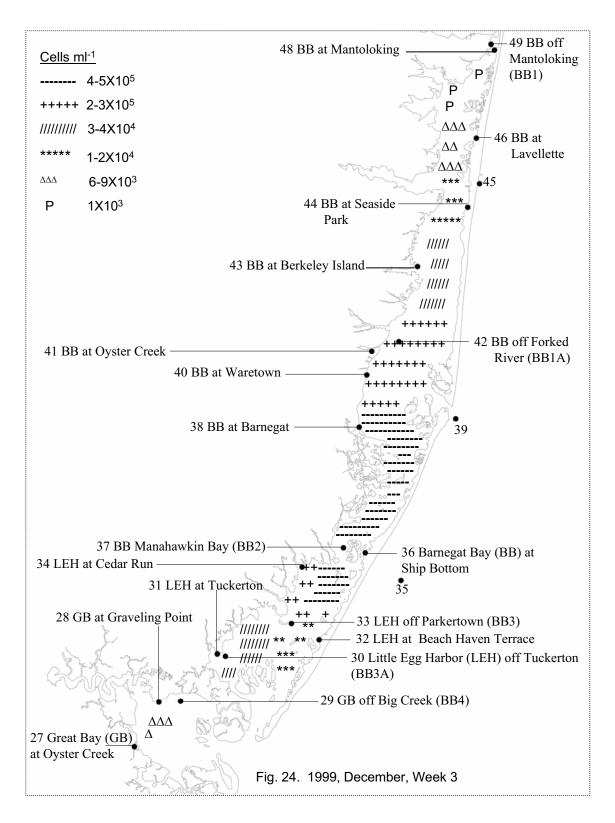


Figure 24. Bloom development in late December, 1999.

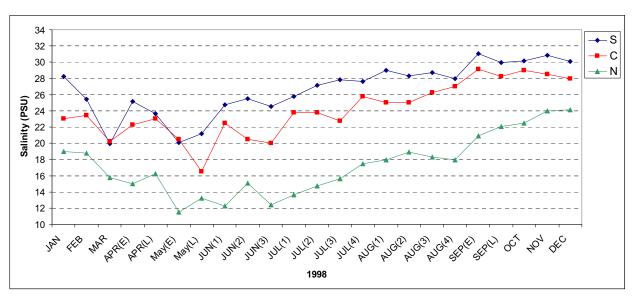


Figure 25. Seasonal change of salinity in the Barnegat Bay-Little Egg Harbor estuarine system and Great Bay in 1998. S, C, N denote South, Central and Northern zones of the survey region. The number following the month identifies the week when sampled; E or L identifies first or second halves of the month.

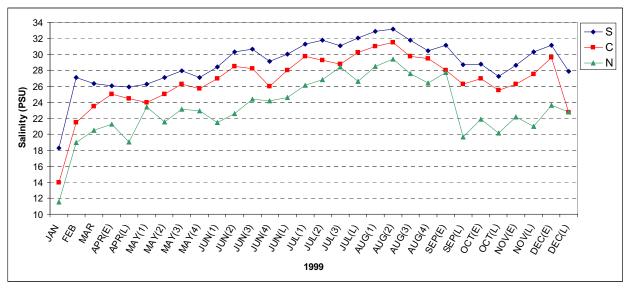


Figure 26. Seasonal change of salinity in the Barnegat Bay-Little Egg Harbor estuarine system and Great Bay in 1999. S, C, N denote South, Central and Northern zones of the survey region. The number following the month identifies the week when sampled; E or L identifies first or second halves of the month.

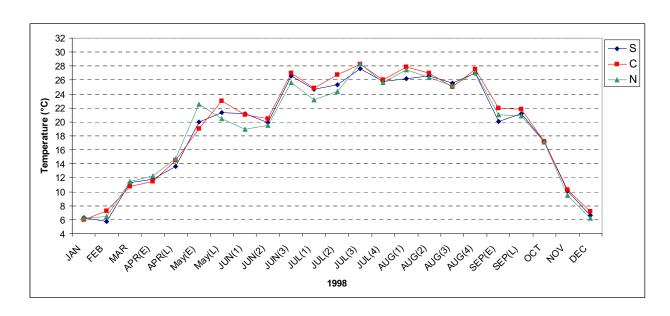


Figure 27. Seasonal change of water temperature in the Barnegat Bay-Little Egg Harbor estuarine system and Great Bay in 1998. S, C, N denote South, Central and Northern zones of the survey region. The number following the month identifies the week when sampled; E or L identifies first or second halves of the month.

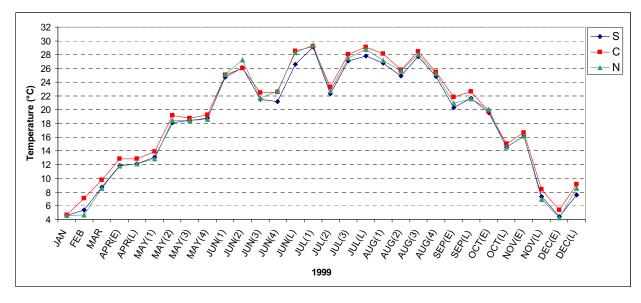


Figure 28. Seasonal change of water temperature in the Barnegat Bay-Little Egg Harbor estuarine system and Great Bay in 1999. S, C, N denote South, Central and Northern zones of the survey region. The number following the month identifies the week when sampled; E or L identifies first or second halves of the month.

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