Phytoplankton production patterns in Massachusetts Bay and the absence of the 1998 winter–spring bloom

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Abstract The seasonal productivity cycle and factors controlling annual variation in the timing and magnitude of the winter–spring bloom were examined for several locations (range: 42°20.35’–42°26.63’N; 70°44.19’–70°56.52’W) in Boston Harbor and Massachusetts Bay, USA, from 1995 to 1999, and compared with earlier published data (1992–1994). Primary productivity (mg C m⁻² day⁻¹) in Massachusetts Bay from 1995 to 1999 was generally characterized by a well-developed winter–spring bloom of several weeks duration, high but variable production during the summer, and a prominent fall bloom. The bulk of production (mg C m⁻³ day⁻¹) typically occurred in the upper 15 m of the water column. At a nearby Boston Harbor station a gradual pattern of increasing areal production from winter through summer was more typical, with the bulk of production restricted to the upper 5 m. Annual productivity in Massachusetts Bay and Boston Harbor ranged from a low of 160 g C m⁻² year⁻¹ to a high of 787 g C m⁻² year⁻¹ from 1992 to 1999. Mean annual productivity was higher (mean = 525 g C m⁻² year⁻¹) and more variable near the harbor entrance than in western Massachusetts Bay. At the harbor station productivity varied more than 3.5-fold (CV = 40%) over an 8 year sampling period. Average annual productivity (305–419 g C m⁻² year⁻¹) and variability around the means (CV = 25–27%) were lower at both the outer nearfield and central nearfield regions of Massachusetts Bay. Annual productivity in 1998 was unusually low at all three sites (<220 g C m⁻² year⁻¹) due to the absence of a winter–spring phytoplankton bloom. Potential factors influencing the occurrence of a spring bloom were investigated. Incident irradiance during the winter–spring period was not significantly different (P > 0.05) among years (1995–1999). The mean photic depth during the bloom period was significantly deeper (P < 0.05) in 1998, signifying greater light availability with depth. Nutrients were also in abundance during the winter–spring of 1998 with stratified conditions not observed until May. In general, the magnitude of the winter–spring bloom in Massachusetts Bay from 1995 to 1999 was significantly correlated with winter water temperature (r² = 0.78) and zooplankton abundance (r² = 0.74) over the bloom period (typically February–April). The absence of the 1998 bloom was associated with higher than average water temperature and elevated levels of zooplankton abundance just prior to, and during, the peak winter–spring bloom period.

Introduction

Water quality data from a temperate, nutrient-enriched bay were examined to determine seasonal productivity patterns and potential factors affecting the timing and magnitude of the winter–spring phytoplankton bloom. Western Massachusetts Bay is the site of an intensive study designed to provide background information to the Massachusetts Water Resources Authority (MWRA) to assess the effect of relocating effluent discharge. Effluents historically released into Boston Harbor have recently (September 2000) been relocated 15 km offshore in shelf water by means of a submarine outfall located at a depth of 32 m. As part of the background study, primary productivity and phytoplankton biomass have been measured using a similar
sampling frequency at two stations (N04, N16 or N18) in the western bay and a third in Boston Harbor (F23) since 1995. These and earlier data (Kelly and Doering 1997) indicate that typically there is a well-developed winter–spring bloom of several weeks duration, variable production during the summer, and a prominent fall bloom. The annual productivity cycle in Massachusetts Bay thus fits the classical pattern generally described for temperate coastal waters (e.g. Cushing 1959; Pratt 1965; Smaya 1973).

Factors recognized as important in controlling the onset of the winter–spring diatom bloom include light, temperature, nutrients, and grazing (e.g. Riley 1967; Smaya 1973; Hitchcock and Smaya 1977; Townsend and Spinard 1986). Research has suggested that the annual winter–spring bloom in temperate areas is controlled by an increase in irradiance coupled with low temperatures that lead to a relaxation in grazing pressure (e.g. Pratt 1965; Martin 1970).

In 1998, a winter–spring bloom did not occur in Massachusetts Bay, and, as a consequence, the annual productivity was the lowest recorded during the 8 year project. Oviatt (1994) and Oviatt et al. (unpublished data) indicated that increased winter water temperature is negatively correlated with the size of the winter–spring phytoplankton bloom in Narragansett Bay, Rhode Island, a temperate coastal area near Massachusetts Bay. A mesocosm study using Narragansett Bay as the parent system similarly indicated a relationship between bloom magnitude and warmer winter temperature (Keller et al. 1999). Bloom magnitude in warm systems was reduced and related to elevated zooplankton abundance and increased grazing (Keller et al. 1999). In Narragansett Bay, water temperature during the winter–spring bloom period has increased in recent years (Oviatt 1994; Keller et al. 1999), and no winter–spring bloom occurred in 1998.

We examined the seasonal productivity cycle in Massachusetts Bay and Boston Harbor prior to effluent diversion using standard 14C techniques (Maestrini et al. 1993). We summarized productivity cycles from 1995 to 1999 and compared them with earlier measurements (Kelly and Doering 1997). We also examined the relationships among potential factors influencing the occurrence of a winter–spring phytoplankton bloom in Massachusetts Bay, including light availability, limiting nutrients, photic depth, mixed layer depth, temperature, and zooplankton abundance.

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**Materials and methods**

**Station locations**

Phytoplankton production was measured at three stations from 1995 through 1999, as part of a large-scale water-quality monitoring program (Fig. 1). Although productivity has been monitored since 1992, during earlier years (1992–1994), there were several modifications in sampling design and productivity measurement techniques (Kelly and Doering 1997). Since 1995, techniques for measuring primary production as well as sample location and frequency have been relatively consistent. Data from these years form the primary data analyzed here. Productivity stations were located along a gradient of decreasing nitrogen concentration from the edge of Boston Harbor into western Massachusetts Bay (Kelly 1997). Station F23 (~24 m depth) is located at the outer edge of Boston Harbor near the recently discontinued MWRA effluent discharge, and has been monitored six to eight times per year since 1995. Station N04 (~49 m depth) is located at the outer edge of a sampling area designated as the “nearfield” region, while stations N16 (~41 m depth) and N18 (~27 m depth) are more centrally located in the nearfield area. The nearfield stations are located in a grid pattern over the new (September 2000) outfall site to monitor water quality in the vicinity of the discharge (Libby et al. 1998). Productivity was typically measured 17 times annually at the nearfield stations (N04, N16, N18). Station N04 was monitored continuously from 1995 to the present, while N16 was sampled in 1995 and 1996 (only six measurements). Station N18, located 2.8 km south of the outfall site, replaced N16 as a productivity station in 1997, because it is in a region more likely influenced by the recently relocated effluent discharge.

**Hydrographic surveys**

Hydrographic surveys have been conducted by MWRA since 1989 to monitor water quality in Massachusetts and Cape Cod Bays. Continuous vertical profiles of the water column and discrete water samples (five depths) were collected using a Sea-Bird SBE-9 CTD/Bottle Rosette system. Standard profiles included measurements for temperature, salinity, density (σt, kg m⁻³), fluorescence, and photosynthetically active irradiation (PAR). Depth (m) of the mixed layer during the winter–spring bloom period was determined from the vertical profiles of σt. Water columns (or the upper portions thereof) were considered vertically homogeneous when density differences (Δσt) were <0.1 kg m⁻³ (Townsend et al. 1992). Light profiles (PAR) were measured using a Biospherical QSP-200L spherical quantum scalar sensor mounted on top of the hydrocast rosette and a Biospherical QSR-240 hemispherical quantum scalar sensor for simultaneous on-deck measurement of incident irradiance (PAR). In situ fluorescence profiles were measured with a Wet Labs WetStar fluorometer.

At each station, discrete depths were typically sampled for dissolved inorganic carbon and nutrients, chlorophyll a (chl a), phytoplankton concentration, and productivity. Zooplankton samples were obtained by vertical-oblique tows of the upper two-thirds of the water column (maximum tow depth 30 m). Additional temperature data were available from a U.S. Geological Service buoy near station N18, with sensors located at the surface, 5 m, and ~20 m.

**Light**

In addition to shipboard measurement of light, irradiance values (FPAR, µE m⁻² s⁻¹) were collected over 15 min intervals at nearby Deer Island using a similar Biospherical QSR-240 sensor. These data were used in the calculation of primary productivity over the daylight period. Daily irradiance values (PAR, E m⁻² day⁻¹) were available from the Deer Island sensor only from 1997 through 1999, and were used to calculate mean (± SD) monthly irradiance (E m⁻² day⁻¹) over this period. Additional light data for comparison among earlier years (1995–1996) during the winter–spring period were available from the Eppley Laboratory (total light, KW·h m⁻² day⁻¹) in Newport, Rhode Island (Hawk 1998). A linear regression comparing mean monthly irradiance between the two sensors was developed using the 1997–1999 data:

\[
\text{Deer Island (PAR) } = 8.6 \times (\text{Eppley, total light}) + 9.51 \quad (r^2 = 0.96), \text{ and used to generate the mean monthly irradiance over the bloom period for 1995–1996.}
\]

To compare underwater light availability among years (1995–1999), light attenuation coefficients (k, m⁻¹) were calculated based
Fig. 1 Water-quality sampling stations in 1995–1999. A grid of 21 stations were in the “nearfield” (N) region in western Massachusetts Bay (inset). “Farfield” (F) stations were located in Boston Harbor, other parts of Massachusetts Bay, and Cape Cod Bay. Productivity was measured at stations labeled “F”: F23, N18 and N04 during 1997–1999. From 1995 to 1997 productivity was measured at station N16 (A) but not N18.

Nutrients

Samples for determination of dissolved inorganic nutrients (NH₄⁺, NO₃⁻, NO₂⁻, SiO₂, PO₄³⁻) were filtered through 47-mm Nucleopore membrane-fiber filters (0.4 μm pore size) and frozen until analysis (<1 month) in 60-ml polyethylene bottles. Samples were analyzed on a Technicon AutoAnalyzer with standard procedures (similar to those of Strickland and Parsons 1972). Primary and secondary standards (in seawater) were used to calculate nutrient concentrations (Oviatt and Hindle 1994). Standard deviations were < 0.05 μmol L⁻¹ for all nutrients measured.

Chlorophyll a

Since 1998 chl a (mg m⁻³) concentrations at productivity stations have been measured by extraction. Replicate chl a samples were filtered through 47-mm Whatman GF/F glass-fiber filters at 125 mmHg maximal vacuum. Two drops of 1% MgCO₃ were added to each sample during filtration. Samples were frozen, extracted by mechanical grinding followed by 2–4 h in 90% acetone at ~20 °C, and analyzed using a Turner Designs model 10AU fluorometer (Yentsch and Menzel 1963). From 1995 to 1997, chl a concentrations at productivity stations were calculated by regression from in situ fluorescence.

Primary production

P–I incubations were undertaken using standard ¹⁴C techniques (Strickland and Parsons 1972). Water samples from five depths (surface, mid-surface, mid-depth, mid-bottom, and bottom) were stored in 1-l dark bottles and kept cool until returned to the laboratory (< 6 h) for incubation. Under dim light, 5-ml subsamples in 20-ml borosilicate vials were inoculated with 1 μCi NaH¹⁴CO₃. Vials (16 light, 2 dark) from each depth were incubated in a light-(250 W Tungsten-halogen lamps attenuated with neutral density
by Dr. J. Turner (University of Massachusetts, Dartmouth) for MWRA with methods described by Albro et al. (1998).

Results and discussion

P–I parameters

The frequency distributions for the maximum hourly production rates per unit biomass ($P_{\text{max}}^B$; assimilation rates, mg C mg$^{-1}$ chl a h$^{-1}$), modeled from incubations in 1995–1999 exhibited the same pattern at the nearfield sites (stations N04, N16 and N18) and the Boston Harbor station (F23). Overall the frequency distribution shows that 71% of the estimates were < 8 mg C mg$^{-1}$ chl a h$^{-1}$ and 79% were < 12 mg C mg$^{-1}$ chl a h$^{-1}$. Nearly all of the estimates for $P_{\text{max}}^B$ (95%) fall below the theoretical maximum (25 mg C mg$^{-1}$ chl a h$^{-1}$, Lohrenz et al. 1994).

Values above the maximum typically occurred when chl a concentrations were very low (< 0.05 mg m$^{-3}$) or when $r^2$ for the P–I curve fit was low (< 0.70). $P_{\text{max}}^B$ averaged 8.0 (median = 5.0) mg C mg$^{-1}$ chl a h$^{-1}$ ($n = 406$) at station N04, 6.9 (median = 3.8) mg C mg$^{-1}$ chl a h$^{-1}$ ($n = 349$) at station N16/N18, and 9.2 (median = 6.6) mg C mg$^{-1}$ chl a h$^{-1}$ ($n = 146$) at station F23. These somewhat elevated rates at the Boston Harbor edge station relative to the nearfield sites may reflect the higher availability of nutrients (average annual DIN was 11.3 μM for 1995–1999 versus < 5 μM for the nearfield sites). Glover (1980) and Côté and Platt (1983) similarly suggested that the biomass-normalized parameters of the P–I curves are partially dependent on nutrient regimes.

$P_{\text{max}}^B$ varied considerably over the seasonal cycle and tended to decrease with depth (particularly during the summer stratified period, May–August) (see for example Fig. 2). Kelly and Doering (1997) noted a similar trend for

Zooplankton abundance

Vertical-oblique zooplankton tows were conducted through the upper 30 m of the water column with a 0.5 m diameter 102 μm mesh net equipped with a flow meter. Zooplankton were preserved in 10% buffered formalin, transferred to 70% ethanol, and reduced to aliquots of at least 300 organisms with a Folsom plankton splitter. Zooplankton were staged, identified (copepodite and adult copepods), and counted. Concentrations of total zooplankton were calculated based on the number of individuals counted, the volume of water sample, and aliquot size. Zooplankton data were collected
decreasing $P_{\text{max}}^{B}$ with depth in 1994 for the same area. In general, peak values occurred during the winter–spring bloom and summer, with rates generally low and invariant during the late fall and early winter (range: 1.0–4.0 mg C m$^{-2}$ h$^{-1}$) (Fig. 2). The mean values (and ranges) for $P_{\text{max}}^{B}$ observed in Massachusetts Bay from 1995 to 1999 are similar to those observed in 1994 (Kelly and Doering 1997) and to values observed in other northeast coastal and estuarine systems (Platt and Jassby 1976; Malone and Neale 1981; Côté and Platt 1983; Pennock and Sharp 1986; Oviatt et al., unpublished data).

The frequency distribution for $z^{B}$ [mg C mg$^{-1}$ chl $a$ m$^{-2}$ h$^{-1}$ (µE m$^{-2}$ s$^{-1}$)$^{-1}$], the initial slope of the $P–I$ curve normalized to biomass, for all stations pooled ($n = 901$), indicates that 83% of the estimates were < 0.1 mg C mg$^{-1}$ chl $a$ m$^{-2}$ h$^{-1}$ (µE m$^{-2}$ s$^{-1}$)$^{-1}$. Fewer than 10% of the values were higher than the theoretical maximum of 0.115 mg C mg$^{-1}$ chl $a$ m$^{-2}$ h$^{-1}$ (µE m$^{-2}$ s$^{-1}$)$^{-1}$ (Schofield et al. 1991; Lohrenz et al. 1994). Values above the theoretical maximum are not unexpected and have been reported by others (cf. Malone and Neale 1981; Lohrenz et al. 1994; Kelly and Doering 1997). Again, high values in the current study were related to low coefficients of determination for the $P–I$ fit or low chl $a$ concentrations. The frequency distributions were similar between the nearfield stations and the Boston Harbor station. The mean and median values for the three sites were very close with a mean of 0.07 (median = 0.04) mg C mg$^{-1}$ chl $a$ m$^{-2}$ h$^{-1}$ (µE m$^{-2}$ s$^{-1}$)$^{-1}$ at station N04, 0.05 (median = 0.03) mg C mg$^{-1}$ chl $a$ m$^{-2}$ h$^{-1}$ (µE m$^{-2}$ s$^{-1}$)$^{-1}$ at station N16/N18, and a mean of 0.06 (median = 0.04) mg C mg$^{-1}$ chl $a$ m$^{-2}$ h$^{-1}$ (µE m$^{-2}$ s$^{-1}$)$^{-1}$ at the Boston Harbor edge station (F23). There was no tendency for $z^{B}$ to increase inshore relative to the nearfield sites. The seasonal cycle is similar to that observed for $P_{\text{max}}^{B}$ with elevated values during the winter–spring bloom and summer, and low values during the fall and late winter (data not shown). The means (and ranges) recorded for the nearfield and harbor edge in 1995–1999 are similar to the values reported for 1994, particularly for the modified mean [0.06 mg C mg$^{-1}$ chl $a$ m$^{-2}$ h$^{-1}$ (µE m$^{-2}$ s$^{-1}$)$^{-1}$] (see Kelly and Doering 1997) and other coastal areas.

### Seasonal production cycle

The annual cycle of vertically integrated water-column productivity (mg C m$^{-2}$ day$^{-1}$) at the nearfield stations (N04, N16, N18) from 1995 to 1999 was generally characterized by a well-developed winter–spring bloom (late February–early April) of several weeks duration, high but variable production during the summer (May–August), and a prominent fall bloom (late August–October) (Fig. 3). Although considerable variability occurred between years and stations, the most notable departures from the typical pattern at the nearfield sites were the absence of a winter–spring bloom in 1998 and a low magnitude bloom in 1995.

![Production - Station N16 - N18](image)

**Fig. 3** Production (mg C m$^{-2}$ day$^{-1}$) at nearfield sites A station N16/N18 and B station N04; and at Boston Harbor site C station F23 over five annual cycles (1995–1999)

At station N16/N18 (Fig. 3A) the winter–spring bloom peak (mean = $\sim$2300 mg C m$^{-2}$ day$^{-1}$) was lower than the fall bloom peak (mean = $\sim$2600 mg C m$^{-2}$ day$^{-1}$) when averaged over 5 years. Production from May through mid-August typically ranged from 1000 to 2000 mg C m$^{-2}$ day$^{-1}$ (mean = $\sim$1500 mg C m$^{-2}$ day$^{-1}$), with values of 300–700 mg C m$^{-2}$ day$^{-1}$ occurring from November through December. The seasonal productivity cycle at station N04 was similar to that observed at N16/N18 (Fig. 3B). The mean production peak at station N04 in the spring (late February–early April) was about the same magnitude as the fall (late August–October) peak ($\sim$2000 mg C m$^{-2}$ day$^{-1}$), but somewhat lower than at station N16/N18. The average production over the 5 year period was 888 mg C m$^{-2}$ day$^{-1}$; this was also lower than at station N16/N18 (mean = 1163 mg C m$^{-2}$ day$^{-1}$) but not significantly different (ANOVA, $P > 0.05$). Most production typically occurred in the upper 15 m of the water column at the nearfield sites.

At the Boston Harbor station (F23) a gradual pattern of increasing production from winter through summer was typical (Fig. 3C), with most production in the upper 5–10 m of the water column. The average productivity measured at F23 from 1995 to 1999 was 1569 mg C m$^{-2}$ day$^{-1}$. Mean productivity at the Boston Harbor station was significantly greater than at the nearfield sites (ANOVA, $F = 13.3$, $P = 0.002$), and station F23 was characterized by significantly higher nutrient concentrations (t-test, $P < 0.05$). Kelly and Doering
(1997) found that average production rates were significantly lower at station F23 than at station N16 in 1994, despite the higher DIN concentrations at the harbor station in 1994. This discrepancy may be tied to methodological differences in measuring productivity between the surveys.

Photic zone depths ($Z_p$, m) were generally shallowest during peak bloom periods (winter–spring and fall) at stations N16/N18, N04, and F23 (Fig. 4). $Z_p$ varied considerably from February to April but was relatively constant during the summer and fall. Mean $Z_p$ over the 5 year period was 10.0 m at station F23 ($n = 30$), 20.5 m at station N18 ($n = 51$), 21.7 m at station N16 ($n = 23$), and 23.4 m at station N04 ($n = 51$). $Z_p$ deepened from station F23 (Boston Harbor) to the outer nearfield station (N04) (Fig. 4). Kelly and Doering (1997) attributed this deepening to approximately equal parts decrease in chlorophyll and non-phytoplankton turbidity from west to east.

Annual productivity

Annual productivity ranged from a low of 160 g C m$^{-2}$ year$^{-1}$ at station N04 in 1998 to a high of 787 g C m$^{-2}$ year$^{-1}$ at station F23 in 1996 over the monitoring period (Table 1). Annual productivity at station F23 was higher (mean = 525 g C m$^{-2}$ year$^{-1}$) and more variable (CV = 40%) than at station N16/N18 (mean = 419 g C m$^{-2}$ year$^{-1}$, CV = 27%) or station N04 (mean = 305 g C m$^{-2}$ year$^{-1}$, CV = 25%). Annual productivity in 1998 was lower than other years at all stations, due largely to the absence of a winter–spring peak in production, which can contribute > 40% of annual production. There were no significant differences in annual productivity among stations when all years were analyzed (ANOVA, $F = 3.03$, $P = 0.07$). When data from 1998 were eliminated from the analysis, annual productivity at station F23 was significantly greater (ANOVA, $F = 4.23$, $P = 0.03$) than at station N04 but not N18.

The relationship between annual production and chl $a$ was investigated by plotting yearly production (g C m$^{-2}$ year$^{-1}$) at each station (F23, N04, N18) versus mean annual chl $a$ (mg m$^{-3}$) for 1998–1999 (Fig. 5). Earlier data (1995–1997) were eliminated from the analysis to avoid variability introduced by methodological differences in chl $a$ determinations. The resulting regression with $n = 6$ and $r^2 = 0.81$ was significant ($P = 0.01$), and indicated a strong linear relationship between annual primary productivity and chl $a$.

Annual estimates for the current period (1995–1999) extend the range of values reported at station F23 from 1992 to 1994 (Kelly and Doering 1997) (Table 1). The

<table>
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$^a$Model results from entire nearfield region (21 stations)

Fig. 4 Photic zone depth (1% PAR, m) at nearfield sites A station N16/N18 and B station N04; and at Boston Harbor site C station F23 over five annual cycles (1995–1999)

Fig. 5 Relationship between annual productivity (g C m$^{-2}$ year$^{-1}$) and mean annual chl $a$ (mg m$^{-3}$) at the productivity stations (F23, N18, N04), 1998–1999
long-term average (1992–1999) at this station (525 g C m⁻² year⁻¹) is at the upper end of the range reported for shelf waters from the Mid-Atlantic Bight to the Gulf of Maine (O’Reilly and Busch 1984) but typical of coastal areas with high nitrogen loading rates (as discussed by Kelly and Doering 1997). The long-term averages for stations N04 (305 g C m⁻² year⁻¹) and N16/N18 (419 g C m⁻² year⁻¹) are lower, and fall within the range reported by O’Reilly and Busch (1984). The long-term average annual productivity decreased with distance from Boston Harbor, which, prior to effluent diversion, exported most of its anthropogenically derived nutrient input to western Massachusetts Bay.

Winter–spring bloom period

The apparent absence of a winter–spring phytoplankton bloom in Massachusetts Bay in 1998 precipitated our examination of the potential factors influencing bloom development for the study area. Blooms occur when phytoplankton populations grow rapidly and reach high biomass (Legrand 1990; Cloern 1996) and primary productivity temporarily exceeds loss processes. Winter–spring blooms begin when the daily surface irradiance reaches a threshold value (Hitchcock and Smaida 1977; Bämstedt 1985). A second critical element in the initiation of a bloom is an available pool of nutrients. Even in the face of sufficient light and abundant nutrients, bloom initiation is dependent on productivity being large relative to all mechanisms of phytoplankton loss, including consumption (grazing) by pelagic and benthic animals (Cloern 1996). Consequently, the timing and magnitude of blooms can be controlled by top down processes, originating at higher trophic levels (Deason and Smaida 1982; Bämstedt 1985). Variations in bloom magnitude are important because of the role of phytoplankton carbon as the base of the marine food chain. High magnitude blooms are associated with the supply of large amounts of organic matter to the bottom, which serves as a rich food source for benthic organisms (Townsend and Cammen 1988; Rudnick 1989; Powell et al. 1995). Low-magnitude blooms result in most of the organic matter going to pelagic consumers, with subsequent alterations in the food web (Keller et al. 1999). Our previous research has suggested that during cool winters (<3 °C in January–March) the reduced metabolic rate and slow development of pelagic organisms minimizes grazing and phytoplankton biomass accumulates. During warm winters, development and grazing by pelagic consumers keep pace with production and low-magnitude blooms are evident (Keller et al. 1999).

We were particularly interested in the observation that there was no phytoplankton bloom in 1998 since our research in Narragansett Bay, Rhode Island similarly indicated the absence of a bloom for that year (Oviatt et al., unpublished data). In Narragansett Bay diminished bloom magnitude has been associated with warmer winter water temperature and increased grazing (Hawk 1998; Keller et al. 1999; Oviatt et al., unpublished data). The productivity pattern characteristic of western Massachusetts Bay includes the development of a major diatom bloom generally in February–early April (Fig. 3), but the magnitude of the bloom has varied from year-to-year, with well-developed blooms occurring in 1996, 1997, and 1999 (Fig. 6). Productivity at the nearfield sites from February through April 1998 was significantly lower than the average production over the bloom period (late February–early April) in 1996, 1997, and 1999, but not 1995 (ANOVA, $F = 6.59, P = 0.03$). Chl $a$–specific productivity was not significantly different among years (ANOVA, $F = 1.08, P > 0.05$), suggesting that the lack of a winter–spring bloom was the result of biomass failing to accumulate rather than reduced specific production rates. Our prior research in marine mesocosms had also suggested that winter–spring production peaks appear to be an effect of high biomass levels rather than increases in specific production rates (Keller 1988).

Light, light attenuation, and mixed layer depth

In general, the initiation of a winter–spring phytoplankton bloom in temperate waters has been tied to the increase in light associated with the progression of seasons. Daily incident irradiance (PAR, E m⁻² day⁻¹) gradually increased over the bloom period in 1998 from a minimum of 2.5 E m⁻² day⁻¹ near the beginning of the period to a maximum of 81.4 E m⁻² day⁻¹ near the end. The average daily irradiance over the bloom period in 1998 (34.5 E m⁻² day⁻¹) was similar to that observed in 1997 (39.6 E m⁻² day⁻¹) and 1999 (38.7 E m⁻² day⁻¹). Monthly averages for 1995–1996 over the bloom period were generated using Eq. 1 and compared across years. Mean monthly irradiance over the bloom period in 1998 was not significantly different from other years.

![Average Production Feb. - Apr.](image)

Fig. 6 Average production (mg C m⁻² day⁻¹) at the nearfield stations (N04, N16/N18) over the winter–spring bloom period (generally late February–early April), 1995–1999. Error bars = ± 1SD.
(ANOVA, $F = 0.03$ $P = 0.87$), suggesting that incident irradiance did not limit bloom initiation in 1998.

We also compared the average attenuation coefficients ($k, \text{m}^{-1}$) and the mean photic depths (1%, m) over the bloom period among years. Light attenuation coefficients were significantly lower (ANOVA, $F = 12.0$, $P = 0.01$) and photic depths significantly deeper (ANOVA, $F = 20.3$, $P = 0.02$) in both 1998 and 1995. The assumption of a constant light attenuation coefficient with depth introduced a 7% error in the estimate of the underwater light field but did not alter the comparison among years. The winter–spring bloom at the nearfield sites typically occurred when the water column was well mixed, prior to the onset of seasonal stratification, which generally occurred in late April. Consequently, attenuation coefficients and photic depths were relatively good indicators of light availability in the water column during the bloom period. The greater light availability with depth during the bloom period in 1995 and 1998 was due to decreased chl $a$ concentration associated with the lack of a winter–spring bloom or its diminished magnitude. Since incident irradiance was equivalent to other years and light at depth was greater, it is apparent that the absence of the winter–spring bloom in 1998 was not a result of insufficient light.

Mixed layer depths ranged from 27.5 to 46.0 m (mean = 38.1 m) during the peak winter–spring bloom periods at stations N04, N16, and N18 over the 5 year period. With the exceptions of station N04 in 1996, 1998, and 1999, winter–spring blooms were observed in the absence of vertical stratification when density differences ($\Delta \rho_s$) were $<0.1$ kg m$^{-3}$ from surface to near-bottom. Townsend et al. (1992) similarly observed a spring bloom in offshore Massachusetts Bay in 1990 in the absence of vertical stratification. Density differences of $\sim0.2$ kg m$^{-3}$ were observed in the water column (bottom depths of $\sim46$ m) at station N04, during bloom peaks in 1996, 1998, and 1999. The corresponding mixed layer depths were 30.5 m ($\Delta \rho_s = 0.02$ kg m$^{-3}$) in 1996, 27.5 m ($\Delta \rho_s = 0.08$ kg m$^{-3}$) in 1998, and 35.0 m ($\Delta \rho_s = 0.01$ kg m$^{-3}$) in 1999. Mixed layer depths were usually, but not always, less than critical depth during the winter–spring bloom peak (exceptions: station N04 in 1997, 1999; station N18 in 1999), as was also observed by Townsend et al. (1992) for the Gulf of Maine. In 1998, the mixed layer depths at stations N04 and N18 were less than the calculated $D_m$ during the period when the winter–spring bloom typically occurred (February–early April) and unrelated to the absence of the bloom.

Dissolved inorganic nitrogen

Figure 8 illustrates the typical drawdown of dissolved inorganic nitrogen (DIN, $\mu$M) in the surface waters of the nearfield region of Massachusetts Bay over the winter–spring bloom period from 1995 to 1999. In general, DIN concentrations were approximately equal in the surface and bottom waters during February with levels typically >5 $\mu$M at stations N04, N16, and N18. By April, surface concentrations were depleted while bottom water concentrations were still relatively high. Actual DIN concentrations in bottom waters may either gradually decrease over time (cf. 1996) or, more rarely, increase (cf. station N16, 1995). The pattern in 1998 was notably different from other years. Concentrations of DIN were similar in surface and bottom waters throughout the winter–spring bloom period. Although DIN concentrations decreased gradually, they did not go below 5 $\mu$M and DIN was not limiting production. Dissolved inorganic silica exhibited a pattern similar to DIN. With the exception of 1998, silica concentration dropped below 3 $\mu$M in surface waters during the bloom period, reaching levels as low as 0.11 $\mu$M in some years (data not shown). In 1998, although silica gradually decreased from initial levels of 10–11 $\mu$M, concentrations remained above 6 $\mu$M in surface waters at station N04 and N18 throughout February–April. Nutrient

Temperature

Our prior research in Narragansett Bay, Rhode Island, has indicated a significant correlation between the magnitude of the winter–spring phytoplankton bloom and temperature (Hawk 1998; Keller et al. 1999; Oviatt et al., unpublished data). In Narragansett Bay when winter water temperature remained above 3°C in the months when winter–spring blooms occurred (generally January–March) reduced blooms were noted. In Massachusetts Bay, the nearfield surface temperatures (<5 m) in 1998 were among the warmest on record (over the bloom period) since 1990 (Fig. 7). Among recent years (1995–1999), surface temperatures in 1998 were significantly warmer than 1996 and 1999 but not 1995 and 1997 (ANOVA, $F = 9.9$, $P = 0.0001$). The presence of significant variability in temperature among years suggests that it may be an important factor controlling bloom magnitude in Massachusetts Bay.

![Fig. 7 Daily temperature (°C) measurements (calculated as the average of hourly values measured by the U.S. Geological Service at a buoy between stations N18 and N21) from January to April, 1990-1999](image)
limitation did not appear to play a role in the absence of a bloom in 1998.

Trophic interactions and temperature

We also examined interactions between warm winter water temperature and observed variation in bloom magnitude and zooplankton abundance in Massachusetts Bay. Initially, we examined the relationship between productivity (mg C m\(^{-2}\) day\(^{-1}\)) during the bloom period and the co-occurring peak phytoplankton biomass (mg chl \(a\) m\(^{-3}\)) from 1995 to 1999 (Fig. 9). Peak bloom production was significantly \(F = 18.3, P = 0.003\)) and positively related to the natural logarithm of peak chl \(a\) concentration over the bloom period. Chl \(a\) has been considered a poor indicator of phytoplankton productivity over a wide range of environmental conditions or aquatic environments (Cadée and Hegeman 1974; Boynton et al. 1982; Cole and Cloern 1984). And yet, within specific embayments or over segments of the seasonal cycle, good correlations (as seen here) occur between production and chl \(a\) (Côté and Platt 1983; Cole and Cloern 1984; Malone et al. 1986; Keller 1988). Productivity during the bloom period in Massachusetts Bay is strongly correlated with phytoplankton biomass rather than with an increase in specific production rates.
We next examined the relationship between bloom biomass measured as depth-averaged chl a during the peak production period and the average surface temperature over the period of the winter–spring phytoplankton bloom (generally late February–early April) (Fig. 10A). The resulting inverse relationship was significant ($F = 28.0$, $P = 0.001$), and indicated that warmer water temperatures during the bloom period (as in 1998) were correlated with reduced bloom magnitude (Fig. 10A). The highest magnitude blooms (> 4.0 mg chl a m$^{-3}$) occurred in the coolest years (1996, 1999, Fig. 10A). We previously described similar results for Narragansett Bay over a longer period of increasing water temperatures (1960–1995) and in a mesocosm study (Oviatt 1994; Keller et al. 1999). In Massachusetts Bay, bloom magnitude appears similarly related to interannual variation in temperature.

Zooplankton abundance, just prior to and during the peak winter–spring bloom (typically late February) was significantly related ($F = 19.9$, $P = 0.003$) to the co-occurring mean surface temperature, with increased abundance associated with higher temperature (as in 1998, Fig. 10B). In a mesocosm experiment examining the impact of elevated temperature on the trophic structure of nutrient-rich coastal systems we found that high zooplankton abundance and low phytoplankton standing stock occurred in warm systems (+3 °C relative to cool) and vice versa (Keller et al. 1999). In Massachusetts Bay, we similarly found that elevated zooplankton abundance was characteristic of warmer temperatures during the bloom period, and was significantly related ($F = 24.2$, $P = 0.002$) to lower phytoplankton standing stock (Fig. 11). In our mesocosm experiment, zooplankton abundance and calculated grazing rates were low in the cool systems (temperature: −1.7 °C to 4.4 °C) and similar to levels previously reported for Narragansett Bay during the winter–spring bloom period (Keller et al. 1999). In warm systems (temperature: 2.5–7.2 °C), the higher grazing rates were more typical of values reported later in the spring–summer (Deason 1980). Even if grazing rates (unmeasured) were not elevated in response to the higher temperatures observed in Massachusetts Bay during the bloom period in 1998 (Fig. 7), we infer that the overall impact of grazing would increase as a result of the greater abundance of zooplankton in warm years (Fig. 10B).
In general, the match or mismatch between periods of production and abundance of phytoplankton and their respective grazers will greatly influence the magnitude of the bloom (Cushing 1982). In coastal areas and on temperate shelves, there has typically been a mismatch between the winter–spring diatom bloom and peak zooplankton abundance. The phytoplankton are not efficiently cropped by the zooplankton but instead sink and provide input to the benthic food web (Walsh 1981; Smetacek et al. 1984). Elevated temperatures during the winter–spring bloom period may have enhanced the match between the peak abundance of phytoplankton and zooplankton (as suggested by Townsend and Cammen 1988), resulting in a reduced bloom biomass in Massachusetts Bay in 1998. In shallower estuaries and coastal embayments, grazing by benthic organisms may also play a role in reduced bloom magnitude (Oviatt et al., unpublished data). In Massachusetts Bay, the absence of a winter–spring bloom in 1998 appears related to the warm surface temperatures associated with a warm El Niño year as well as increased abundance of zooplankton and inferred higher grazing rates.

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