



# Annual Primary Production in Narragansett Bay with no Bay-Wide Winter–Spring Phytoplankton Bloom

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Received 30 October 2000 and accepted in revised form 25 May 2001

Primary production was estimated over the annual cycle from  $^{14}\text{C}$  incubations conducted in 5 m deep enclosures and modeled for 16 stations in Narragansett Bay with data from biweekly surveys in which light, chlorophyll, attenuation coefficients and other parameters were measured. Annual values ranged from  $160 \text{ g C m}^{-2} \text{ y}^{-1}$  in the lower West Passage to  $619 \text{ g C m}^{-2} \text{ y}^{-1}$  at the mouth of the Providence River. The annual bay-wide, area mean fell near the middle of this range at  $323 \text{ g C m}^{-2} \text{ y}^{-1}$  and was not apparently different from previous surveys. In the 1998 warm, El Niño winter, no bay-wide winter–spring phytoplankton flowered. Bloom limitation was correlated with warm temperatures which may have stimulated grazing rates. The lack of a bloom did not change annual levels of primary production but this alteration in carbon flow may impact macrofauna in the benthic infauna community.

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**Keywords:** phytoplankton; climate trends; warming; primary production; nutrients;  $^{14}\text{C}$

## Introduction

Historically, the winter–spring diatom flowering has been the signature ecological event in Narragansett Bay. In the 1960s, Pratt (1965) described logarithmic growth beginning usually in December, and after a month, terminating at a maximum sometimes exceeding  $50\,000 \text{ cells ml}^{-1}$ . This prodigious growth of cells and biomass was unique in the seasonal cycle where cell densities did not typically exceed  $10\,000 \text{ cells ml}^{-1}$ . Smayda (1973) notes an annual temperature range of  $-1^\circ$  to  $25^\circ \text{C}$  and suggested the lower temperatures were consistent with the occurrence of boreal–arctic plankton species in Narragansett Bay, the southern–most extension of this thermal group along the eastern seaboard. During the first 17 years of monitoring from the 1950s he found a seasonal succession during the diatom flowering of *Detonula confervacea* succeeded by *Thalassiosira nordenskiöldi* which was replaced by *Skeletonema costatum*. After 1970, other species sometimes dominated along with variations in bloom initiation and duration causing him to suggest that the environment might be changing. Since the 1970s the winter–spring bloom has been reduced in duration and intensity or failed to occur (Oviatt 1994). The question arises as to whether this reduction in phytoplankton biomass has had any effect on annual levels of primary

production or on other trophic levels within the ecosystem.

Two estimations of primary production measured by  $^{14}\text{C}$  for separate locations within the bay and a synoptic survey of oxygen net production have been made. A primary production value by the  $^{14}\text{C}$  method of  $310 \text{ g C m}^{-2} \text{ y}^{-1}$  (Furnas *et al.*, 1976) was obtained using water samples collected at one location near the middle of the West Passage and incubated on-shore in a light gradient box. Keller (1988) reported primary production values by the  $^{14}\text{C}$  method of 250, 165, and  $150 \text{ g C m}^{-2} \text{ y}^{-1}$  using water collected over 3 years from the lower West Passage and incubated in a 5 m deep enclosure. In a survey conducted in 1971–1973, oxygen light and dark bottles were incubated *in situ* at 3 to 5 stations in three sectors of the Bay biweekly over the annual cycle resulting in a bay-wide area average net estimate of  $269 \text{ g C m}^{-2} \text{ y}^{-1}$  (Oviatt *et al.*, 1981).

The current applicability of these primary production estimates has been placed in doubt by changes in the bay. Since 1970, water temperatures have increased, ammonia concentrations have increased, phosphate concentrations have decreased and chlorophyll concentrations have decreased (Hawk, pers. comm.). A weakened winter–spring bloom has been correlated with higher winter water temperatures ( $r^2=0.39$ , Oviatt, 1994; Keller *et al.*, 1999). Questions remain about how much organic matter produced in the winter falls to the sediment to support the benthic

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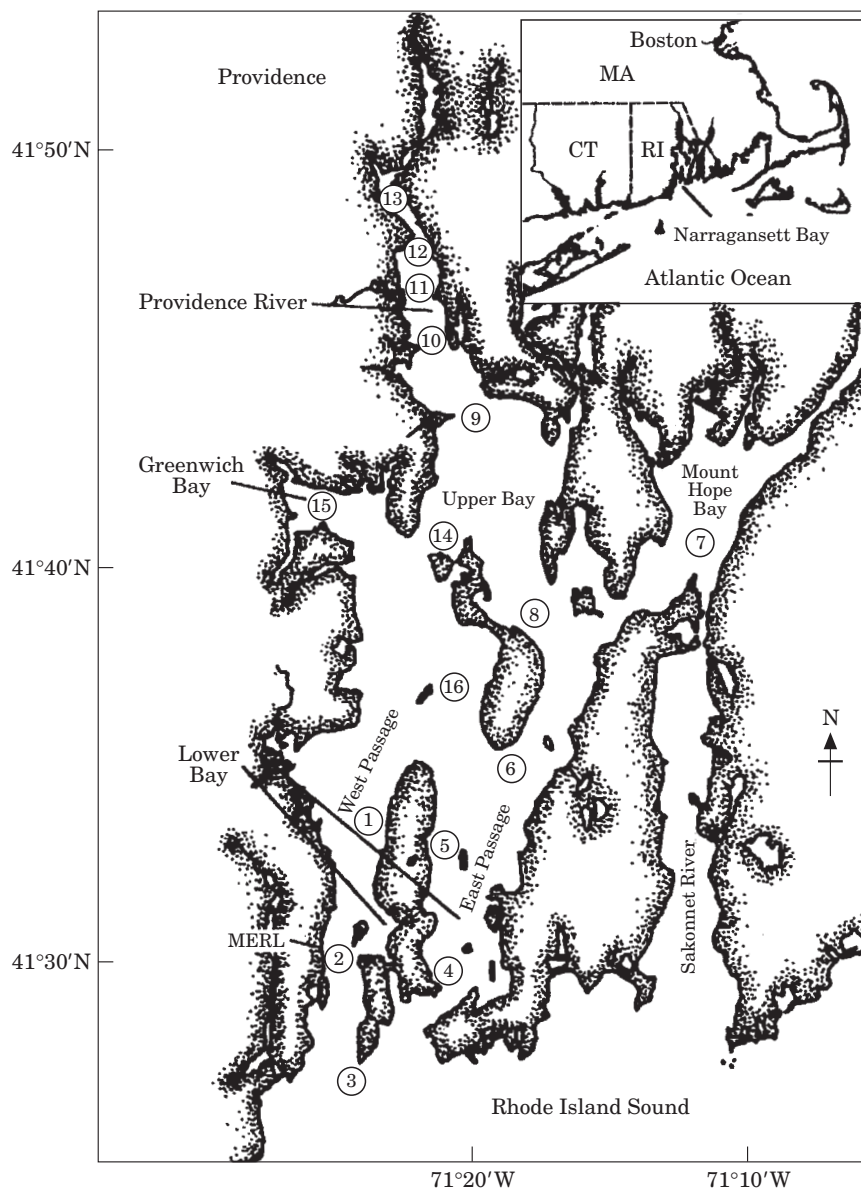


FIGURE 1. Location of Bay Survey Stations from April 1997 through April 1998. Water for  $^{14}\text{C}$  incubations was collected from stations 1, 5 and 11. Photosynthetic parameter curve fits from these incubations were applied to survey stations 14, 15, 16, 1, and 2 for water incubations from station 1, to survey stations 3 to 8 for water incubations from station 5 and to survey stations 9 to 15 for water incubations from station 11.

infauna community over the warmer months. For this study, our objectives were to estimate synoptic values for primary production in Narragansett Bay, using a standard  $^{14}\text{C}$  technique (Maestrini *et al.*, 1993), and to assess the reasons for the lack of a winter–spring bloom.

### Methods

Every two weeks from April 1997 through April 1998 16 stations were occupied throughout Narragansett

Bay independent of tides (Figure 1). Station locations were determined by visual ranges and a Geographical Positioning System (GPS) to within  $\pm 25$  m. Vertical profiles of temperature, oxygen, and salinity were taken with a YSI 600 Sonde Unit. Irradiance was measured at the surface and through the water column with a LiCor 193 SA,  $4\pi$  spherical quantum sensor. For each station profile, an attenuation coefficient ( $k$ ) was determined by regressing  $\ln(I_z/I_0)$  vs. depth, with  $I_0$  the surface (0.1 m below the water) irradiance and  $I_z$  the irradiance at depth  $z$

(m). The slope of the regression line estimates  $k$  ( $m^{-1}$ ).

Water samples for chlorophyll, total nitrogen (TN), and total phosphorus (TP) were taken by a Niskin Bottle 1 m below the surface and 1 m off the bottom. For chlorophyll samples, the water (10 ml) was filtered through 25 mm glass fibre filters and frozen until analysis. Filters were subsequently extracted in 10 ml of 90% acetone, in the dark, within a refrigerator for 24 h. Concentrations were calculated using the equations of Lorenzen (1966) modified to correct for instrument drift. The coefficients of variation on replicated samples was 2.7% (Oviatt & Hindle, 1994).

Whole water nutrient samples (40 ml) were placed in opaque plastic bottles, held over ice, and frozen until analysis for total nutrients including dissolved, particulate, organic and inorganic forms. Total Nitrogen and Phosphorous (TN and TP) were measured using the persulphate digestion technique of Valderamma (1981). Concentrations of  $NO_2+NO_3$  and  $PO_4$  were measured colorometrically on a Technicon Autoanalyzer. Precision was  $\pm 0.1 \mu M$  N at the  $10 \mu M$  level of N,  $\pm 0.3 \mu M$  N at the  $60 \mu M$  level of N and  $\pm 0.3 \mu M$  P at the  $1 \mu M$  level of P.

Within 1 day of each bay-wide survey phytoplankton production ( $^{14}C$ ) was measured on a sunny day using water collected from three regions in the bay. Surface water samples were taken from near shore early in the morning at station 1 in the West Passage (boat launch at Frigate Street), station 5 in the East Passage (Carr Lane), and station 11 in the Providence River (Rhode Island Yacht Club) (Figure 1). The rate of carbon uptake was determined by a modified method of Steemann Nielsen (1952). Glass bottles (300 ml) were filled with water from each station and inoculated with  $2.5 \mu Ci ml^{-1}$  sodium ( $^{14}C$ ) carbonate. Bottles for each station were suspended at 18 depths to precisely define the decrease of production with irradiance attenuation in a 5 m deep (13 000 l) enclosure in natural sunlight and exposed for about 2 h around noon. Samples for all three incubations were simultaneously hung from three separate ropes suspended 30 cm from the centre of the enclosure and equidistant from each other. Three dark bottles were suspended at 4.5 m. The ropes holding the bottles at 18 fixed depths were rotated horizontally at 5 rpm (3 min in one direction; reverse for 3 min in the opposite direction) to mix the samples. After incubation, the bottles were filtered through 47 mm glass fibre filters. The activity of the filters was determined by an internal quench standard, liquid scintillation count in triplicate using ('Cytoscint') cocktail. Primary production in  $mg C m^{-3} h^{-1}$  (averaged over the incubation period) was calculated according to

Strickland and Parsons (1972). The detection limit was  $0.01 mg C m^{-3} h^{-1}$  and the reproducibility was 10% at  $5 mg C m^{-3} h^{-1}$  (Oviatt & Hindle, 1994).

Sunlight was measured continuously during the day of incubation and summed hourly and daily by a LiCor 190 SA Cosine Quantum Sensor. Underwater light profiles were measured with a LiCor 192 SA Cosine Underwater Quantum Sensor. Irradiance in the water column of the enclosure, which was used to estimate the photosynthesis *vs.* irradiance (P-I) curves, was corrected to approximate the irradiance measured using the  $4\pi$  collector in the field. A series of dual measurements yielded the empirical relationship:

$$\text{Irradiance (4}\pi \text{ collector)} = 1.046 \text{ Irradiance (cosine collector)} - 0.040, R^2 = 0.99$$

This step was necessary to apply P-I curves fit to the enclosure data to the field measurements (see below). The corrected underwater irradiance was used to calculate  $k$  (the attenuation coefficient) as described for the survey data.

Water samples for chlorophyll were taken from each of the 3 locations and analysed as during the surveys. Dark corrected hourly production values were plotted against irradiance intensity. Two models were used to fit the incubation data. The first model was a three parameter model which included a photoinhibition term following Platt *et al.* (1980):

$$P = P_{SB} (1 - e^{-a}) e^{-b}$$

with  $P$  as production ( $mg C m^{-3} h^{-1}$ ),  $P_{SB}$  as the theoretical maximum production without photoinhibition ( $mg C m^{-3} h^{-1}$ ),  $a = a/I/P_{SB}$ ,  $b = \beta I/P_{SB}$ , and  $a$  is the initial slope of the P-I curve (units of  $mg C E^{-1} m^{-1}$ ),  $I$  is irradiance ( $E m^{-2} h^{-1}$ ), and  $\beta$  is the photoinhibition term (same units as  $a$ ).

If the three parameter model did not converge, the data were fit to a two-parameter model without photoinhibition (Webb *et al.*, 1974):

$$P = P_{max} [1 - e^{-aI/P_{max}}]$$

with  $P_{max}$  the light saturated maximal productivity and  $a$  the initial slope of the curve. The modified Gauss-Newton non-linear least-squares technique (SAS) was used to provide the best fit of the data to the above equation.

Individual station productions were calculated by first normalizing P-I values to chlorophyll levels at the three water collection stations; the normalized values were multiplied by the chlorophyll values from the 16 survey stations to yield production in  $g C m^{-3} h^{-1}$ .

TABLE 1. Photosynthetic parameters summary

Location	(n) Mean $P_{\max}$ ( $\pm$ SE) ( $\text{mg C m}^{-3} \text{ h}^{-1}$ )	Mean $PB_{\max}$ ( $\pm$ SE) ( $\text{mg C mg Chl}^{-1} \text{ h}^{-1}$ )	(n) Mean alpha ( $\pm$ SE) ( $\text{mg C E}^{-1} \text{ m}^{-1}$ )	(n) Beta ( $\pm$ SE) ( $\text{mg C E}^{-1} \text{ m}^{-1}$ )
Providence River	(23) 41.6 ( $\pm$ 10.6)	5.5 ( $\pm$ 1.6)	(23) 0.17 ( $\pm$ 0.036)	(5) 0.002 ( $\pm$ 0.001)
West Passage	(24) 11.4 ( $\pm$ 1.6)	3.5 ( $\pm$ 0.6)	(24) 0.08 ( $\pm$ 0.013)	(3) 0.006 ( $\pm$ 0.003)
East Passage	(24) 9.0 ( $\pm$ 1.7)	3.4 ( $\pm$ 0.021)	(24) 0.07 ( $\pm$ 0.021)	(3) 0.003 ( $\pm$ 0.001)

Thus, hourly irradiance, attenuation coefficients and chlorophyll from each survey station were combined with the fitted  $P$  vs.  $I$  relationship for each region to calculate hourly primary production ( $\text{mg C m}^{-3} \text{ h}^{-1}$ ) for each station. The set of model parameters utilized for each station was based on the proximity of that station to one of the three regions where water was collected for incubations (Figure 1). Hourly production rates were calculated for each hour of the day, integrated over photic depth (1% light level) and summed to give daily rates ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ).

Surface chlorophyll values were used throughout the modeling exercise to calculate hourly and daily production. In winter in the Providence River and Upper Bay, surface and bottom chlorophyll values were similar. During summer, the attenuation of irradiance with depth limited productivity to the surface mixed layer. During summer surface and bottom chlorophyll values varied by up to two orders of magnitude in the Providence River and Upper Bay and up to a factor of two in the West and East Passages.

Dissolved inorganic carbon analysis for the  $^{14}\text{C}$  calculation was performed on an O.I. Corporation model 700 Total Carbon Analyser using purge and trap methodology (McKenna & Doering, 1995). Concentrations were calculated from standard curves generated from dilutions of a primary solution of  $\text{NaCO}_3$  ( $8.826 \text{ g NaCO}_3 \text{ l}^{-1}$  of deionized water).

The intensity of stratification for each station at each sampling was estimated by differences in sigma  $t$  between surface and bottom waters. Sigma  $t$  was estimated from temperature and salinity using tables from the U.S. Hydrographic Office (1952).

Water samples for long-term measurement of chlorophyll from lower Narragansett Bay have been taken at weekly intervals since August 1976 to observe trends over time. Samples were not collected from October through December 1977 and from April and May 1981. During 1977 and 1978 samples were taken by Niskin bottle from a depth of 2 m; thereafter, samples were taken from an intake tank supplying input water to an enclosure facility. The

intake is located beneath the Graduate School of Oceanography dock at a depth of 2–3 m (depending on tide); the residence time in the tank is about 15 min and the tank is well-mixed.

Samples for chlorophyll  $a$  were measured as in the survey and calculated according to the equations of Lorenzen (1966) modified to correct for instrument drift. Prior to July 1989, all chlorophyll determinations were made using a Turner Model III fluorometer; subsequent measurements, after comparison inter-calibrations, were undertaken with a Turner Designs Model 10 series field fluorometer. A comparison of 10 replicate measurements yielded a value of 3.46 (coefficient of variation 4.1%) on Model III and a value of 3.45 (coefficient of variation 4.4%) on Model 10 (Oviatt & Hindle, 1994).

## Results

### *Photosynthesis vs. irradiance relationships*

A total of 75 curve fits were performed biweekly from April 1997 to April 1998. Most of the parameters had acceptable standard errors for  $P_{\max}$  ( $\pm 25\%$  of the mean) and  $\alpha \pm 21\%$  of the mean) (Table 1). In the Providence River, where primary production values had the widest range,  $P_{\max}$  had an average standard error of the curve fit of  $\pm 5\%$  and  $\alpha$  had an average standard error of the curve fit of  $\pm 9\%$ . Up to five incubations conducted from late January to late March indicated photoinhibition (i.e. non-zero beta values generated by model fitting) (Figure 2, Table 1). Generally, the values for  $P_{\max}$  and alpha were highest in the nutrient rich Providence River although this was not true during winter–spring 1998 (example shown in Figure 2). Chlorophyll specific  $P_{\max}$  was highest for the Providence River and West Passage and lower for the East Passage (Table 1).

### *Survey and production patterns*

The patterns of salinity and temperature over the annual cycle at stations throughout Narragansett Bay indicate a range of mixed to stratified conditions

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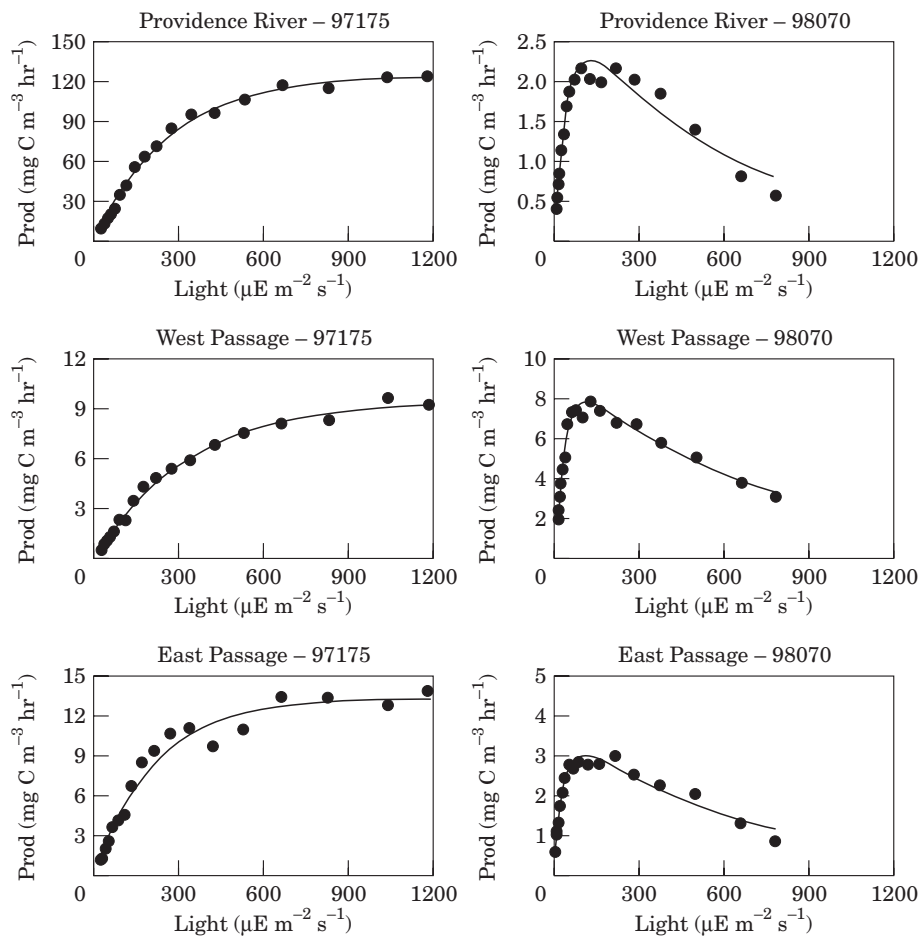


FIGURE 2.  $P$  vs.  $I$  relationships for 24 June 1997 (day 97175) and 8 April 1998 (day 98070). (a) For 24 June 1997 in the Providence River (station 11),  $P_{\max}=125 (\pm 2.59)$ ,  $\alpha=0.463 (\pm 0.017)$ ,  $r^2=0.99$  can be contrasted with the West Passage (station 1)  $P_{\max}=9.8 (\pm 0.207)$ ,  $\alpha=0.029 (\pm 0.0008)$ ,  $r^2=0.99$  and the East Passage (station 5)  $P_{\max} 13.5 (\pm 0.277)$ ,  $\alpha 0.061 (\pm 0.002)$ ,  $r^2=0.97$ . (b) For 8 April 1998, photoinhibition occurred in the Providence River (station 11);  $\beta=0.005 (\pm 0.0006)$ , the West Passage (station 1)  $\beta=0.012 (\pm 0.004)$  and the East Passage (station 5)  $\beta=0.005 (\pm 0.0008)$ . Values in parentheses are  $\pm$  standard errors.

(Figure 3). During 1998, winter–spring salinity differences between surface and bottom waters indicated strong stratification in the Providence River, Upper Bay and Mount Hope Bay ( $\sigma_t$  difference  $\sim 6$ ), indicating considerable fresh water runoff (Figure 3; USHO, 1952). A persistent difference in salinity and temperature indicated moderate stratification at most locations in summer. A more mixed condition predominated in late spring and fall in Greenwich Bay ( $\sigma_t$  difference  $\sim 0.5$ ), West Passage, and to a lesser extent, East Passage. In Rhode Island Sound the seasonal salinity ranged from 29 to 31 psu; whereas in the Providence River, it ranged from 8 to 31 psu (Figure 3). Temperature ranged from 3.5 to 20 °C in Rhode Island Sound and from 3.5 to 26 °C in the Providence River (Figure 3). The warm winter temperatures throughout the Bay correlated with the

strong El Niño event during the 1997–1998 winter (NOAA–CIRES Climate Diagnostics Center) and is consistent with a trend of warmer temperatures since the 1960s (mean 2.2 °C) and 1970s (mean 3.2 °C) compared to the 1990s (mean 3.7 °C) (NOAA gauge Newport and GSO temperature data).

Phytoplankton biomass and production reached highest levels in the Providence River (over  $75 \mu\text{g l}^{-1}$  chlorophyll) and lowest levels in Rhode Island Sound (generally less than  $5 \mu\text{g l}^{-1}$  chlorophyll) and was correlated with the north–south, nutrient concentration gradient in Narragansett Bay (Figures 4–6). Values peaked in summer and were minimum in late fall and winter in the Providence River. In the West and East Passage spring peaks ( $\sim$  day 100) and fall peaks ( $\sim$  day 275) have slightly higher phytoplankton biomass and production than mid summer. These

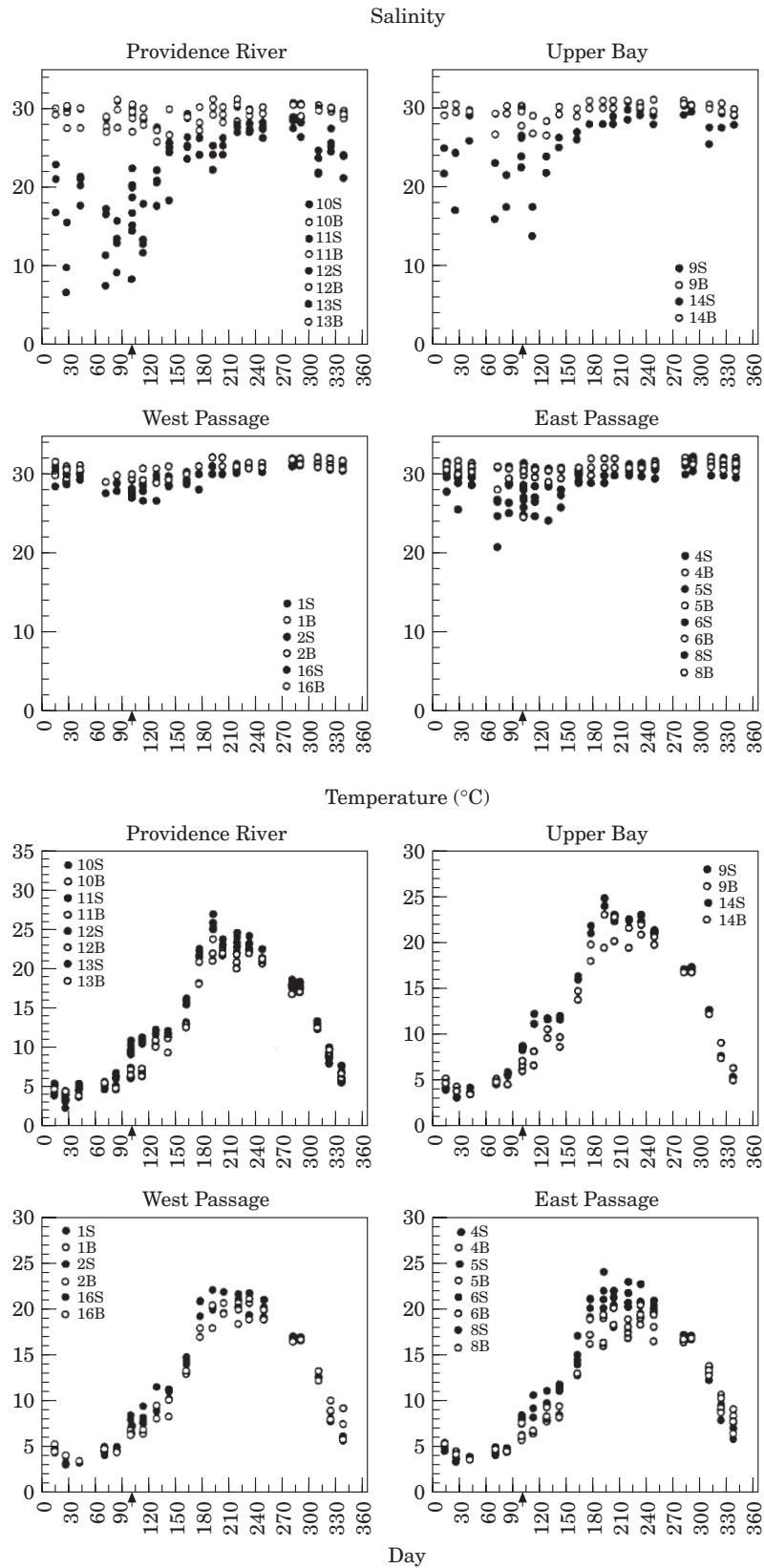


FIGURE 3. Surface, (S) and bottom, (B) salinities, (PSU) and temperature, ( $^{\circ}\text{C}$ ) over the survey year. Station locations included in each figure noted by number, see Figure 1. Note the x axis is day of the year with 1997 data starting after day 100 and 1998 data starting for day 1 to 100. Arrow at the bottom indicates beginning/end of the survey year. Data for stations 3, 7 and 15 are not shown.

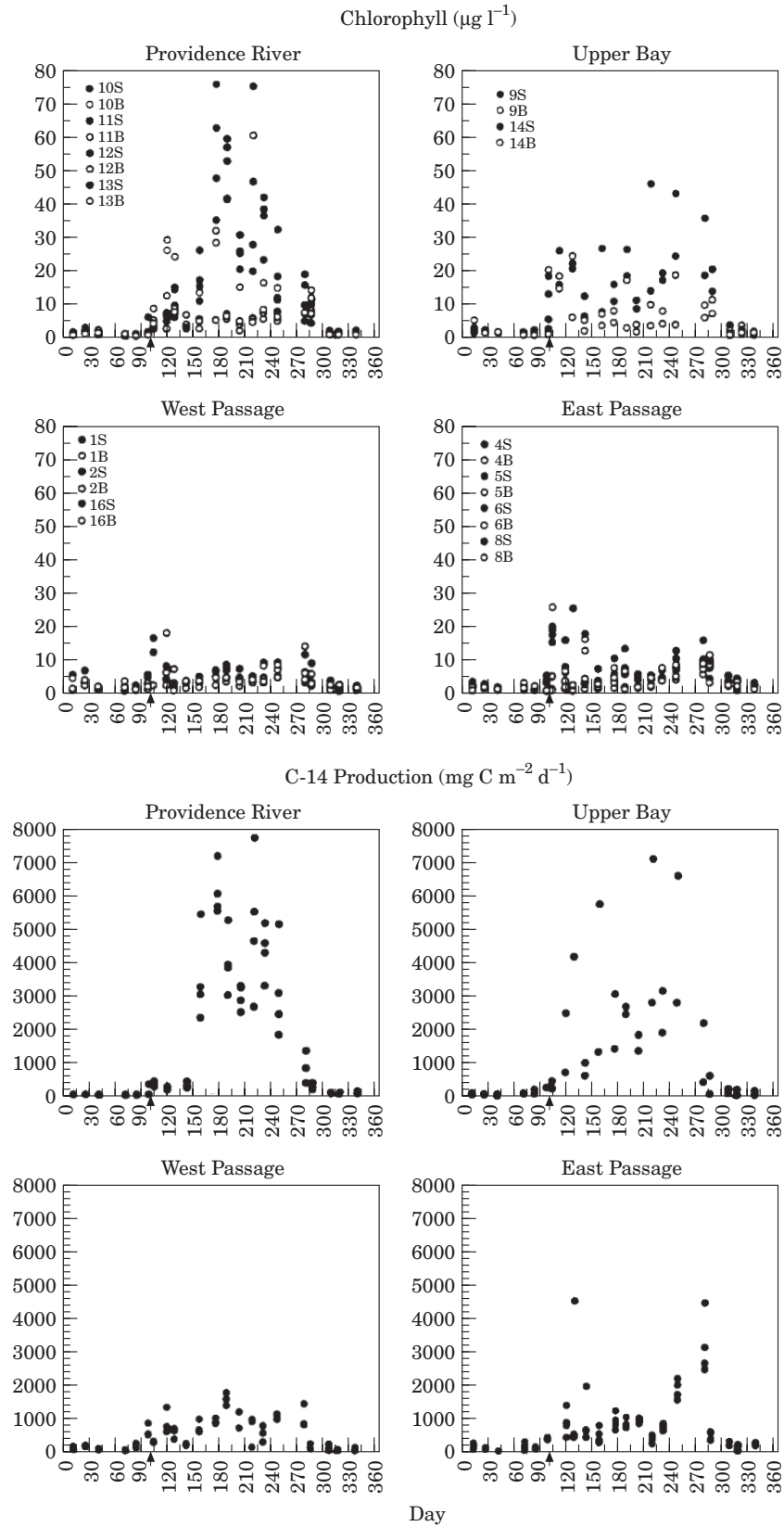


FIGURE 4. Surface, (S) and bottom, (B) chlorophyll,  $\mu\text{g l}^{-1}$  and  $^{14}\text{C}$  production,  $\text{mg C m}^{-2} \text{d}^{-1}$  over the survey year. Primary production has been estimated for all the survey stations of the chlorophyll graphs. Station locations included in each figure noted by number, see Figure 1. Note the lack of a winter-spring bloom at all locations. See legend Figure 3 for x-axis.

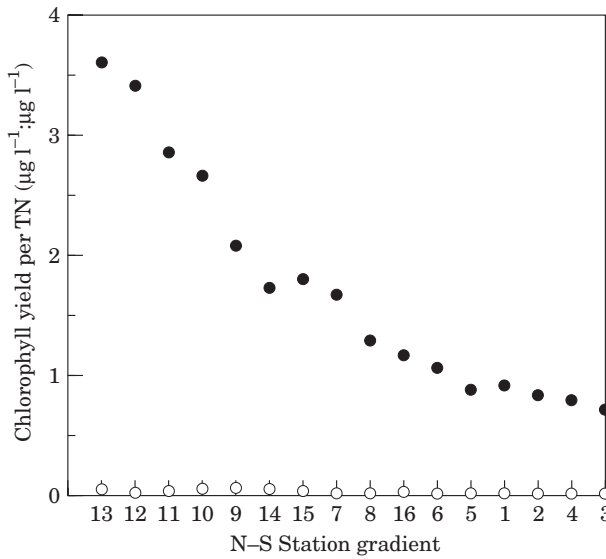


FIGURE 5. Mean chlorophyll, ( $\mu\text{g l}^{-1}$ ) yield at each station normalized by mean total nitrogen concentration (TN), ( $\mu\text{g l}^{-1}$ ) during winter and summer in a north - south gradient along the axis of Narragansett Bay. Actual station numbers noted on the x-axis.  $\circ$  Winter;  $\bullet$  Summer.

production peaks appear more prominent in the East Passage than in the West Passage; in both passages, summer biomass and production exceed winter values.

Total nitrogen (TN) values were maximum in the Providence River and Upper Bay ( $100 \mu\text{M}$ ) due to sewage sources with the minimum observed in Rhode Island Sound ( $20 \mu\text{M}$ ). A similar pattern was seen for total phosphorous (TP) with maximum values of  $10 \mu\text{M}$  in the Providence River and Upper Bay and a minimum value of  $1 \mu\text{M}$  in Rhode Island Sound. Average nutrient values from the current survey agree well with previous values (Pilson & Hunt, 1988). An exception to this agreement was apparently lower TP values in mid to lower bay stations in the current survey year compared to 1986 (not shown). Weak seasonal patterns of reduced TN in summer and elevated TP in summer occurred resulting in total nutrient ratios suggesting no nutrient limitation in winter (TN : TP=22) and nitrogen limitation in summer (TN : TP=6) (Guilford & Hecky, 2000). Summer power relationships between total nutrients and chlorophyll for average values from bay stations explained high degrees of variation in phytoplankton biomass (Mean log Chl,  $\mu\text{g l}^{-1}=1.43$  mean log TN,  $\mu\text{g l}^{-1} - 2.57$ ;  $R^2 = 0.92$ ; mean log Chl,  $\mu\text{g l}^{-1}=1.05$  mean log TP,  $\mu\text{g l}^{-1} - 0.95$ ;  $R^2=0.95$ ). The summer station order for chlorophyll yield revealed highest yields to lowest yield along the north-south axis of the bay which correlated with the

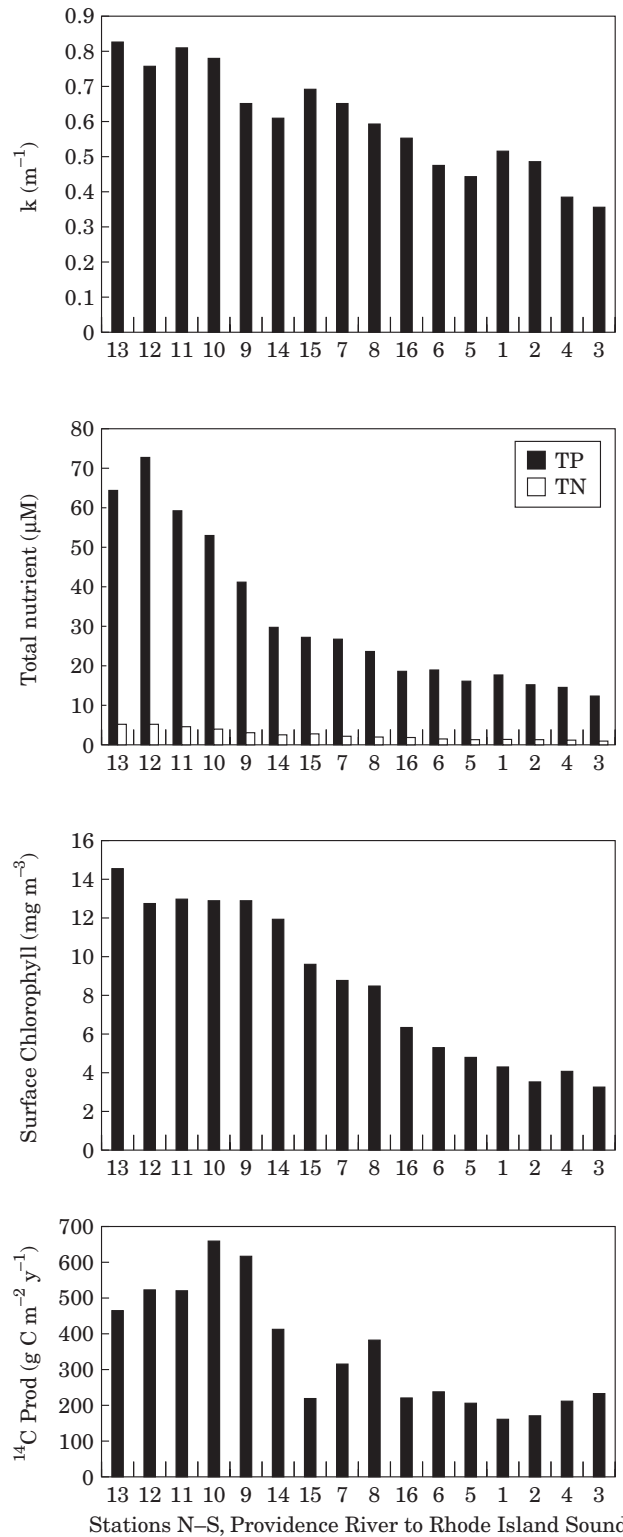


FIGURE 6. North to south gradient of bay survey stations for annual mean attenuation coefficients, ( $\text{m}^{-1}$ ), average winter to summer total nutrients,  $\mu\text{M}$ , annual mean chlorophyll, ( $\mu\text{g l}^{-1}$ ) and annual mean  $^{14}\text{C}$  productivity, ( $\text{g C m}^{-2} \text{y}^{-1}$ ).

TABLE 2. Summary of 1997–1998 C-14 production estimates ( $\text{g C m}^{-2} \text{y}^{-1}$ ) for Narragansett Bay and comparison to Oviatt *et al.* (1981) net oxygen estimates using a P.Q. of 1.2 (Oviatt *et al.* 1986b) for 1971–1973

Location	1997–1998 Mean	1971–1973 Mean
Providence River	559	429
Station 9	619	
Station 10	662	
Station 11	523	
Station 12	524	
Station 13	466	
Upper Bay	517	—
Station 9	619	
Station 14	415	
Greenwich Bay 15	219–254	
Mt Hope Bay 7	315	
West Passage	241	277
Station 1	160	
Station 2	169	
Station 14	415	
Station 16	219	
East Passage	258	218
Station 4	210	
Station 5	204	
Station 6	237	
Station 8	381	
Rhode Island Sound 3	232	
Narragansett Bay (area based mean)	323	269

attenuation coefficient gradient (Figures 5 and 6). By contrast, the winter station order for chlorophyll yield showed no relationship to the north–south gradient and low yield for all nutrient levels (Figures 5 and 6).

#### Estimated production

Estimated daily primary production mirrored the gradients in chlorophyll and nutrient concentrations with highest values in the Providence River and lowest values down Narragansett Bay (Figures 4 and 6, Table 2). Production values were highest in the summer in the Providence River, Upper Bay and West Passage. Annual estimates for primary production by the  $^{14}\text{C}$  method ranged from 160–662  $\text{g C m}^{-2} \text{y}^{-1}$  from the lower West Passage to the lower region of the Providence River, respectively (Table 2). Values further up the Providence River decreased to 524  $\text{g C m}^{-2} \text{y}^{-1}$ . Values for the Upper Bay exceeded values for Mount Hope Bay and Greenwich Bay (Table 2). Values for Greenwich Bay were esti-

ated using P *vs.* I parameters from both the West Passage and the Providence River resulting in a range of values from 219–254  $\text{g C m}^{-2} \text{y}^{-1}$ , respectively. Deeper stations in Rhode Island Sound and the East Passage tended to have higher values than the more shallow lower West Passage. Area estimates for Narragansett Bay (Kremer & Nixon, 1978) were used to determine a bay-wide mean of 323  $\text{g C m}^{-2} \text{y}^{-1}$ .

#### North–south productivity gradient

When the survey stations were ordered north to south along the nutrient gradient from the Providence River to Rhode Island Sound, values decreased in a regular or stepped manner (Figure 6). Mean light attenuation coefficients, *k*, decreased from about 0.83 in a regular manner to 0.35 at Rhode Island Sound; mean nutrients decreased by 75% from the Providence River to Rhode Island Sound; mean chlorophyll dropped from a Providence River plateau of 13  $\mu\text{g l}^{-1}$  in a regular decrease to about 3  $\mu\text{g l}^{-1}$  at Rhode Island Sound; C-14 production showed less evenness but dropped from a high of about 600  $\text{g C m}^{-2} \text{y}^{-1}$  in the Providence River to about 200  $\text{g C m}^{-2} \text{y}^{-1}$  in the Lower Bay.

#### Winter–spring phytoplankton bloom

A bay-wide winter–spring phytoplankton bloom failed to occur in winter–spring 1998 when water temperatures remained above 3.5 °C (Figures 3 and 4). Evidence of a bloom, by chlorophyll but not primary production by  $^{14}\text{C}$ , was apparent in early January in Greenwich Bay (Figure 7). Other stations had slight elevations in chlorophyll: Upper Bay station 8; West Passage stations 16, 1, and 2; and East Passage Station 5 (Figure 7). Providence River stations, Upper Bay stations 9 and 14, Mt. Hope Bay and East Passage Stations showed no increase in chlorophyll (Figure 4). The historical record of chlorophyll data from the lower West Passage indicated intense winter–spring blooms at temperatures less than 3.5 °C although less intense blooms may sometimes occur at the elevated temperature (see 1986, Figure 8).

## Discussion

#### Annual production comparisons

Different techniques of measurement may not distinguish, with great sensitivity, whether primary production between years are different. Production estimations for the 1997–1998 survey based on  $^{14}\text{C}$

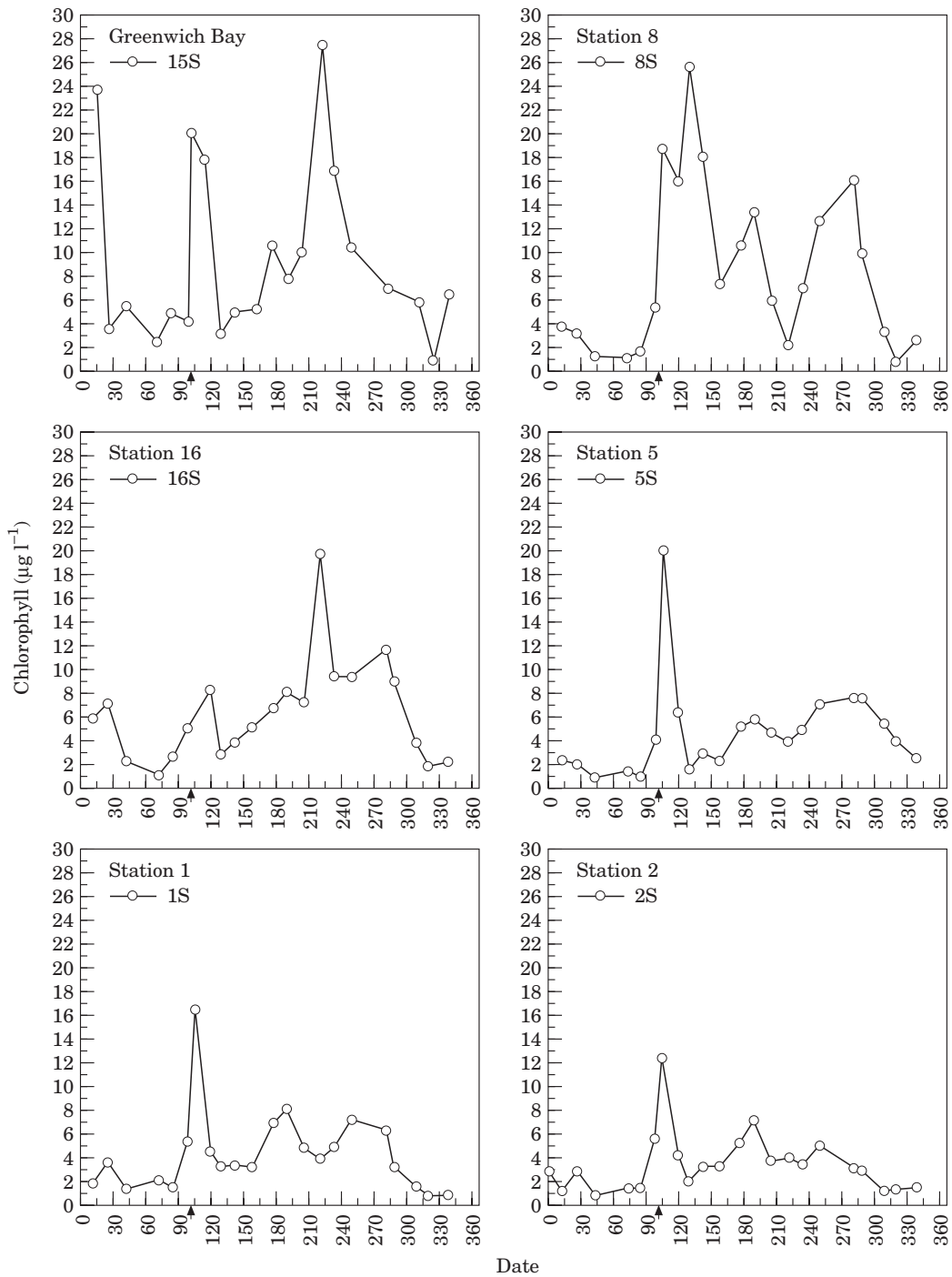


FIGURE 7. Seasonal chlorophyll concentrations (open circles) at stations showing evidence of a usually, minimal winter-spring bloom in 1998. Note time axis as in Figure 3.

were about 17% higher than estimations for the 1971–1973 survey based on oxygen (Table 2). While the photosynthetic quotient (P.Q.) can vary widely on individual dates and locations, an integrated value using a large data set, gave a value of 1.2 for

Narragansett Bay (Oviatt *et al.*, 1986b). Using this conversion of 1.2, the bay-wide, area-based average for this survey period appears to be higher by  $50 \text{ g C m}^{-2} \text{ y}^{-1}$  compared to the earlier net estimate based on oxygen (Table 2). Short-term (2 h)  $^{14}\text{C}$

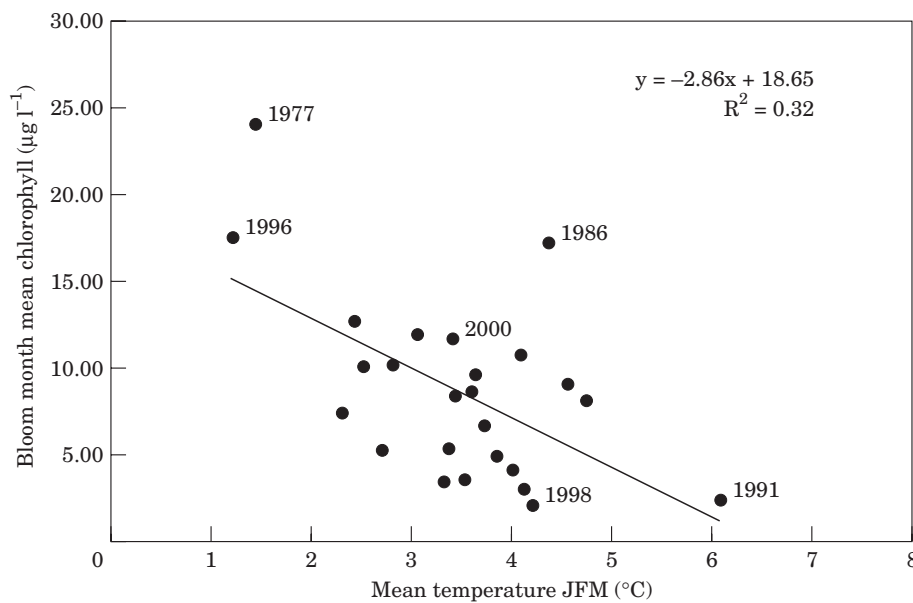


FIGURE 8. Winter mean water temperature versus chlorophyll concentration (mean highest value over a four week period) during the winter-spring diatom bloom in Narragansett Bay over the last 20 years, updated from Oviatt (1994). Note the 1977 bay-wide bloom with a mean value of  $24 \mu\text{g l}^{-1}$  in January which continued through February and March like the signature blooms of the 1950s and 1960s (Pratt, 1965; Smayda, 1973). Also note the February bloom of 1996 when water temperatures were similarly cold.

incubations may be measuring closer to gross production (Harris, 1978) than the net production reported for the oxygen based estimations (Oviatt *et al.*, 1981). The net oxygen mid-day hourly values were converted to daytime values using the Vollenweider (1966) conversion (i.e.  $\sim 57\%$  of daily net phytoplankton production occurs between 1000 and 1400h) or about seven times the hourly mid-day rate; whereas the  $^{14}\text{C}$  mid-day, hourly values converted to the modelled daytime value by an irradiance factor of about nine. A dawn to dusk  $^{14}\text{C}$  incubation (6 October 1998) reaffirmed the approximate factor of nine with an hourly rate of  $0.066 \text{ g C m}^{-2} \text{ h}^{-1}$  and a daily rate of  $0.570 \text{ g C m}^{-2} \text{ d}^{-1}$ . When the Vollenweider factor of seven was applied to the  $^{14}\text{C}$  estimation in this survey, the apparent gross value of  $323 \text{ g C m}^{-2} \text{ y}^{-1}$  drops to an apparent net value of  $251 \text{ g C m}^{-2} \text{ y}^{-1}$ . This net estimate was close to the average for northeast estuaries. Net production in northeast estuaries varies from low values around 170 (Long Island Sound, Hudson River) to mean values around 250 (Bedford Basin, Peconic Bay) to high values around 300–350 (Raritan Bay, mid Chesapeake Bay) in  $\text{g C m}^{-2} \text{ y}^{-1}$  (Day *et al.*, 1987). The apparent net production value for Narragansett Bay of  $251 \text{ g C m}^{-2} \text{ y}^{-1}$  may be compared with the net production of  $269 \text{ g C m}^{-2} \text{ y}^{-1}$  of the earlier survey period, a difference of 7%. No difference between the two survey periods can be ascertained.

#### Temperature and winter-spring bloom dynamics

Despite the lack of differences in annual primary production in the 2 survey years, the winter patterns of production do appear to have changed. In the warm, wet El Niño 1997–1998 year of the survey, no bay-wide winter-spring phytoplankton bloom occurred. The distinctive phytoplankton pattern characteristic of Narragansett Bay is the development of a major diatom bloom from December through April (Pratt, 1965; Smayda, 1973). Even in non-bloom years, diatoms dominate in winter months. While no cell counts were available for January 1998, rough counts in January 1999 with no bloom indicated only  $90\,500 \text{ cells l}^{-1}$  with over half being diatom species; in the January 2000 mini-bloom, the total cell counts were 1.7 million per litre and almost all diatoms, dominated by *Eucampia zodiacus*, *Skeletonema costatum*, *Chaetoceros* spp. and others (Paul Hargraves, pers. comm.). Although nutrients were plentiful, the factors correlated with the lack of phytoplankton flowering in 1998 include a high flushing rate, low light levels and temperature elevated grazing rates.

Nutrient limitation was not considered to be the limiting factor in bloom development since nutrients typically reach their highest annual concentrations in winter and since chlorophyll yield per total nutrient was low through the winter spring period (Figure 5).

TABLE 3. Calculated flushing time in days for 1998<sup>a</sup> using river flow from USGS and equations in Asselin and Spaulding, 1998, and Pilson, 1985

Month 1998	Providence River <sup>b</sup>	Narragansett Bay <sup>c</sup>
January	1.8	18
February	1.3	15
March	0.6	12
April	2.0	21

<sup>a</sup>1998 Blackstone River flow at Woonsocket, USGS, R. Socolow pers. comm.

<sup>b</sup>Asselin and Spaulding, 1993.

<sup>c</sup>Pilson, 1985.

TN ranged from 40 to 100  $\mu\text{M}$  in the Providence River and Upper Bay and from 20–30  $\mu\text{M}$  in the passages in January; TP ranged from 1 to 3  $\mu\text{M}$  in both locations in January (data not shown). Chlorophyll yield per total nutrient has been used as an ecosystem descriptor, originally in lakes (Sakomoto, 1966), to indicate nutrient status (Dillon & Rigler, 1974) and grazing pressure limits on chlorophyll yield (Meeuwig *et al.*, 1998). Typically, marine waters show less chlorophyll yield per unit total nutrients than fresh waters, even though these concentrations are well below those observed in fresh waters, indicating chlorophyll may be limited by factors other than nutrients (Guildford & Hecky, 2000). In Narragansett Bay, the chlorophyll yield (calculated as the mean ratio of chlorophyll to total nitrogen by station) was low in winter at all stations and according to the nutrient gradient, high in northern portions of the bay and lower in southern portions in summer (Figure 5). In summer, the regression relationship for chlorophyll yield from Narragansett Bay [ $y$  (mean log chl,  $\mu\text{g l}^{-1}$ ) =  $1.43$  (mean log TN,  $\mu\text{g l}^{-1}$ ) -  $2.57$ ;  $r^2=0.92$ ] was almost identical to Japan's lakes ( $y=1.4 \times -2.5$ , Sakomoto, 1966) indicating remarkable consistency across ecosystems for the summer period. However, the winter low chlorophyll yield suggests nutrients were not controlling phytoplankton biomass at this time.

While a high precipitation and flushing rate occurred in the rivers during winter–spring 1998, these factors would not have prevented a bloom in the bay. If phytoplankton have a doubling time of 0.5–1.0 per day at temperatures less than 5 °C (Eppley, 1972), flushing times of 0.6 to 2.0 days in the Seekonk and Providence Rivers during spring 1998 may have prevented blooms in the Providence River region (Table 3). Flushing would not have prevented blooms throughout the rest of the bay where residence time ranged between 15 and 18 days in January and February (Table 3).

Irradiance may also limit bloom initiation but could only have delayed the bloom in winter 1998. Hitchcock and Smayda (1977) reported a delayed winter–spring bloom in 1973 due to low light; the bloom occurred in February. Using their method of calculation for light in the water column and light data from Eppley Laboratories (James Hawk, pers. comm.), their limiting irradiance level was not exceeded until March 1998. However, even with a 50% increase in irradiance in March, the bloom failed to occur.

Over the past 25 years, winter water temperatures have risen by about 2 °C provoking the hypothesis that grazing may control the winter–spring phytoplankton bloom (Oviatt, 1994). In warmer winters of the 1980s to 1990s when water temperatures have remained above 3 °C, reduced blooms have occurred, as in this survey year (Figure 8). In consequence, annual mean chlorophyll concentration in the mid West Passage has apparently decreased more than 2  $\mu\text{g l}^{-1}$  over the period from 1973 to 1990 (James Hawk, pers. comm.; Li & Smayda, 1998).

#### *Evidence for grazing*

Experimental studies in mesocosms with elevated winter temperatures have shown that zooplankton grazing or benthic grazing or both may control the winter–spring diatom bloom (Keller *et al.*, 1999). Concurrent with an eighteen year decline in annual phytoplankton biomass, Li and Smayda (1998) found a doubling of zooplankton dry weight supporting the hypothesis that zooplankton grazing may be a top down control on phytoplankton. Zooplankton grazing has been shown to be responsible for the decline of the winter–spring bloom in previous studies (Martin, 1965). During warm winters zooplankton may even prevent the initiation of the winter–spring bloom (Keller *et al.*, 1999). The low winter values of chlorophyll yield (Figure 5) can be interpreted as a function of temperature elevated grazing during the 1998 winter–spring period. Depending on mixing and lack of stratification, benthic areas and intertidal areas with high populations of suspension feeders and filter feeders might contribute along with zooplankton to grazing control of bloom dynamics (Keller *et al.*, 1999).

Exceptions like 1986, when a winter–spring bloom occurred in a warm winter, can be instructive with respect to the grazing hypothesis (Figure 8). During much of 1985 Narragansett Bay experienced a brown tide bloom by *Aureococcus anophagefferens* (Keller & Rice, 1989). Filter feeders such as mussels, scallops and quahogs starved on this poor food source and

failed to reproduce that year (Tracy *et al.*, 1988). While no data exist, zooplankton also probably starved on the tiny cells of the brown tide species. By winter, we speculate, no grazers were present. While 1986 was a warm winter, the grazer abundance was too low to prevent a winter–spring phytoplankton bloom (Figure 8).

#### Impact on benthic infauna

Most of the carbon produced in the winter–spring diatom bloom during cold years falls to the bottom ungrazed to form detrital food for deposit feeding infauna for the following year (Parsons *et al.*, 1984; Rudnick & Oviatt, 1986). This carbon fall has been estimated in mesocosm experiments for Narragansett Bay at 31–50 g C m<sup>-2</sup> (Rudnick & Oviatt, 1986). Estimates for other areas have ranged from 6 g C m<sup>-2</sup> (Baltic), 8.2 g C m<sup>-2</sup> (Long Island Sound), to 11–70 g C m<sup>-2</sup> (Kiel) as cited in Riebesell (1989). A year of reduced detrital carbon supply may result in reduced summer infauna as the food runs out (Grassle *et al.*, 1985). Alternatively, this pattern could be explained by summer predation by epibenthic shrimp and fish (Sandra T. Whitehouse, pers. comm.). Further studies will be required to resolve the importance of these different explanations.

#### Acknowledgements

We gratefully acknowledge the help of graduate students James Hawk and Tarquin Dorrington, and the help of technicians Edwin Requentina, Eric Klos and Gwynne Holcombe. Dr Donald Webb acted as Radiation Safety Officer for this work. Erika Nicosia calculated sigma *t* values to indicate density differences between surface and bottom waters. Peter Doering reviewed the manuscript and made several suggestions for improvement. We thank the Sea Grant Program for supplemental support for nutrient analyses, for completing the annual cycle of measurements and for inter-comparison measurements. This work was supported by Project Number R/ES-972 from the Rhode Island Sea Grant Program.

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