

The importance of light in the initiation of the 1972-1973 winter-spring diatom bloom in Narragansett Bay¹

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Abstract

In 1972-1973 the winter-spring phytoplankton maximum in Narragansett Bay was delayed until late February; it usually occurs in December. Incident light intensity levels relative to the 15-year mean were unusually low until mid-January and increased thereafter through February. Inception of the bloom in mid-January occurred shortly after the estimated in situ intensity of 40 ly d^{-1} was attained—the critical intensity suggested by Riley required to initiate the spring bloom in temperate coastal waters. Low incident and in situ light intensity, rather than temperature or, as in previous years, a relaxation of grazing pressure, appeared to cause the unusually late bloom inception during 1972-1973.

The phytoplankton of Narragansett Bay has been studied continuously for two decades (Ferrara 1953; Smayda 1957, 1973; Pratt 1959, 1965). A large winter-spring bloom of diatoms usually begins in mid-December (Pratt 1965), with logarithmic growth continuing thereafter for as long as a month, followed by a series of pulses and eventual termination of the bloom in May-June. This bloom occurs earlier than in the contiguous waters of Block Island Sound (Riley 1952) and Long Island Sound, where the classical spring bloom occurs.

The factors contributing to this early bloom inception in Narragansett Bay include its shallow depth, its mixing characteristics, and a low flushing rate (Smayda 1957). Pratt (1965) related annual variations in the date of bloom inception to zooplankton abundance. Some subsequent in vitro grazing experiments have strengthened the hypothesis that a relaxation in grazing pressure can regulate the start of this bloom (Martin 1970). However, simulated in situ experiments during the 1972-1973 winter-spring bloom suggest that grazing did not prevent the population increase of the diatom *Skeletonema costatum*, which initiated this bloom (Vargo 1976). The concentration of copepods in the bay varied little during the prebloom period (Hulsizer 1976), yet the

bloom did not commence until mid-January 1973 and reached its first maximum in late February. Smayda (1973) has demonstrated that low temperatures can inhibit the growth of *S. costatum*. This report evaluates the role of other factors, particularly light intensity, in controlling the inception of this delayed bloom.

We acknowledge the helpful review received from G. A. Riley. B. Coyne typed the manuscript and drafted the figures.

Methods

Weekly samples were collected with Niskin bottles in lower Narragansett Bay at a site identical to Pratt's (1965) station 2 from 4 December 1972 to 26 February 1973. Samples were collected near the bottom (ca. 8-m depth), middepth (4 m), and surface, and equal volumes from each depth were then mixed to create a pooled sample. There is little, if any, stratification in Narragansett Bay during winter months (Smayda 1957); hence, this procedure is believed to give a representative sampling of the mixed layer at station 2. Chlorophyll *a* was determined on the pooled sample using Lorenzen's (1966) fluorometric technique. Daily light intensities for December through February were obtained from the Eppley Laboratories, Newport, Rhode Island, 9 km away.

The average daily radiation in situ at station 2 was calculated by Riley's (1957, 1967) equation:

¹ This study was supported by National Science Foundation grant GA 31319X.

$$\langle I \rangle = \frac{I_0}{kz}(1 - e^{-kz}),$$

where $\langle I \rangle$ (ly d^{-1}) is the mean amount of light received by the phytoplankton in a well mixed water column of depth z (in meters) and extinction coefficient k . I_0 is the daily incident radiation. The extinction coefficient, k , was determined from Secchi disk readings made weekly at the time of sampling. The equation for transforming the depth of disappearance of the Secchi disk to k was that of Holmes (1970):

$$k = \frac{1.44}{Z_{sd}},$$

where Z_{sd} is the depth of disappearance. This equation, a revised form of that given by Poole and Atkins (1929), is more appropriate for turbid coastal waters. Temperature was recorded for each depth at the time of collection and averaged to give a mean value for the water column.

Results

The chlorophyll *a* content of the pooled sample during the 13-week sampling period gradually decreased from a high initial level ($3.26 \mu\text{g liter}^{-1}$) on 4 December to concentrations of about $1 \mu\text{g liter}^{-1}$ which persisted through mid-January (Table 1, Fig. 1). The increased chlorophyll level accompanying initiation of the winter-spring bloom thereafter is evident, including the notable increase from about 7.5 to $25.1 \mu\text{g liter}^{-1}$ during late February. The bloom then was dominated by *Detonula confervacea* ($5,000 \text{ cells ml}^{-1}$), which first appeared in February, *S. costatum* ($3,800 \text{ cells ml}^{-1}$), which had persisted since December, and several species of *Thalassiosira*, including *T. nordenskioeldii* ($660 \text{ cells ml}^{-1}$), which appeared in February.

During December 1972, the average daily incident radiation for the week preceding the weekly sampling date varied from 152.3 ly d^{-1} during the first week to 63.8 during the fourth week (Table 1); temperature decreased during the same time from 6.5° to 4.1°C . Although January 1973 was also a cloudy month, the av-

Table 1. Weekly light, temperature, chlorophyll, and zooplankton levels at station 2 from December 1972-February 1973.

	$\langle I_0 \rangle^*$	k^\dagger	$^\circ\text{C}$	$\mu\text{g Chl } a/l$	ZPL \ddagger
4 Dec	152.3	0.58	6.5	3.26	12.2
11	62.8	0.44	5.9	2.00	27.4
18	121.4	0.82	4.1	1.89	20.3
26	63.8	0.41	4.1	0.51	15.5
2 Jan	98.8	0.44	4.8	1.18	29.7
8	125.3	0.64	2.2	1.02	13.0
15	200.6	0.41	1.4	0.83	62.5
23	185.9	0.55	4.5	2.50	22.2
29	136.2	0.58	4.1	4.13	16.2
5 Feb	175.6	0.41	4.0	4.25	114.9
12	175.9	0.72	0.8	4.50	25.7
19	254.0	0.48	1.3	7.49	73.5
26	295.6	0.72	1.9	25.2	40.3

* Average daily incident light intensity as ly day^{-1} for 7 days preceding sampling date.

† Extinction coefficient (m^{-1}).

‡ Zooplankton biomass as mg m^{-3} collected with a No. 10 net.

erage daily radiation usually exceeded December levels. It increased from 98.8 ly d^{-1} from the first to the third week (200.6 ly d^{-1}) and decreased thereafter to 136.2 during the fifth week (Table 1). Average water temperature at station 2 progressively decreased from 4.8° to 1.4°C in mid-January and thereafter increased to above 4°C . In February the average daily radiation increased from 175.6 ly d^{-1} during the week before the sample was collected on 5 February to 295.6 during the week before the 26 February sample, the final sampling date (Table 1). The temperature decreased from 4°C on the first sampling date to ca. 1°C on the second and third sampling dates, rising to 1.9°C by the end of February.

Figure 1 shows the estimated average daily light intensity received by the phytoplankton cells in the well mixed, 8-m water column at station 2 and the weekly variations. In December the average incident radiation was low (Table 1), which is reflected in the low ($<20 \text{ ly d}^{-1}$) level of radiation in the water column during the last 3 weeks of this month. In early January the average daily incident radiation was similar to December levels, with a

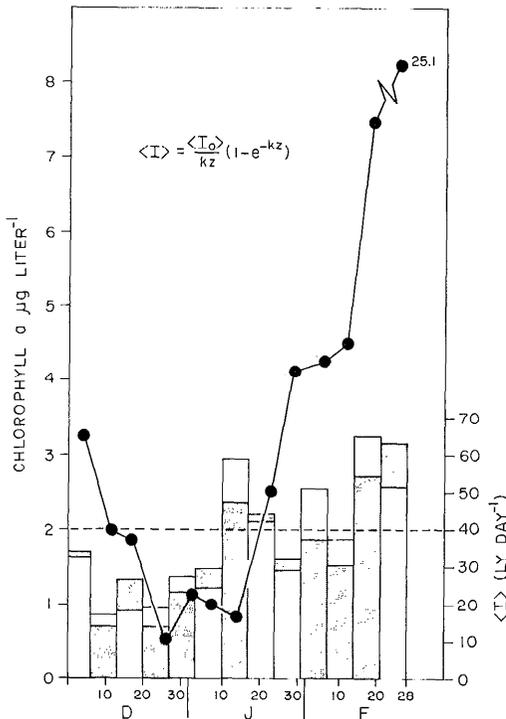


Fig. 1. Concentration of chlorophyll *a* and estimated mean in situ light intensity (I) received by a phytoplankton cell during week preceding sampling date (\bullet) at station 2 from December 1972–February 1973. (I) estimated from extinction coefficient determined on sampling date (open histogram) and from monthly mean (shaded histogram).

large increase noted in midmonth. The average in situ radiation first exceeded 40 ly d⁻¹, the intensity suggested by Riley (1967) as the critical level for spring blooms in coastal estuaries, during the third week of January. Although the estimated in situ radiation dropped below 40 ly d⁻¹ twice after the middle of January, this critical level was exceeded during most of the following weeks. This increased light intensity in situ was mostly a function of increased incident radiation, since the extinction coefficient for the 6 weeks before mid-January (mean 0.56, range 0.41–0.82) differed little from that in the 7 weeks after mid-January (mean 0.55, range 0.41–0.72) (Table 1).

Discussion

The 1972–1973 winter–spring bloom in Narragansett Bay initiated by *S. costatum* was atypical: it did not begin until mid-January, nearly a month later than most of the blooms studied previously. Several factors could have contributed to this late initiation, including nutrients, temperature, light, and grazing. Bioassay experiments (Hitchcock and Smayda 1977) indicate that nutrients, characterized by an annual maximum preceding the winter–spring bloom, did not limit *Skeletonema*'s growth until February.

Laboratory and field experiments have demonstrated that the growth rate of *S. costatum* is less than 1 division per day at temperatures below 3°C (Smayda 1973). Low temperatures have apparently limited its growth in Narragansett Bay during January and February in previous years (Smayda 1973). Therefore, since *Skeletonema* initiates the bloom in Narragansett Bay, low temperatures conceivably delayed bloom initiation in 1972–1973. However, the temperature range of 4°–6.5°C noted during December (Table 1) favored growth rates of from 1.1 to 1.4 divisions per day (Smayda 1973) and, except for mid-January, about 1 division per day would be expected through early February. The period of logarithmic growth in situ began when the water temperature was 2°–4°C (Table 1). Unless hydrographic effects are responsible for the large increase in chlorophyll *a* (25.2 µg liter⁻¹) at the end of February (Fig. 1, Table 1), maximum growth occurred during the period of lowest temperatures, 1°–2°C. Thus, it would appear that temperature had little direct effect on the date of the 1972–1973 winter–spring bloom inception.

Light intensity may have significantly influenced the inception of the 1972–1973 bloom. Pratt (1965) evaluated the factors controlling inception of the winter–spring blooms in this bay from 1959–1960 through 1962–1963 and noted that the incident radiation varied from 122–173 ly

Table 2. Average daily incident ($\langle I_0 \rangle$) radiation (ly d^{-1}) during the winter-spring bloom and its deviation (Δ) from corresponding 15-year mean for Narragansett Bay.

	$\langle I_0 \rangle$	Δ		$\langle I_0 \rangle$	Δ
Dec I	110.8	-24.4	Feb I	227.7	+35.4
II	86.7	-38.6	II	175.9	-35.0
III	85.1	-36.0	III	254.0	+ 9.4
IV	81.9	-47.8	IV	295.6	+42.2
Jan I	140.6	-20.2	Mar I	218.9	-50.8
II	200.7	+32.5	II	199.9	-81.2
III	173.9	+ 2.4	III	201.2	-87.2
IV	148.2	-17.0	IV	314.7	-28.3

d^{-1} at station 2 for the 2 weeks preceding log growth. These periods were all in mid-December. In December 1972 the mean incident radiation was only 91 ly d^{-1} , which was 53-75% that recorded during Pratt's study. Smayda (1973) reported that the mean of 112 ly d^{-1} during December 1971 may have limited the growth of *S. costatum* then. The incident radiation during December 1972 and periodically thereafter was considerably below the 15-year mean computed for each week (Table 2). In fact, this period may be characterized as a "dark" year.

Riley (1967) suggested that 40 ly d^{-1} is the critical intensity required in situ before a spring bloom can occur in a temperate coastal estuary. The estimated in situ intensity ($\langle I \rangle$) during December 1972 to mid-January 1973 was about 50% of the level suggested by Riley, except for the first week in December (Fig. 1). Thus, Riley's equation and suggested critical intensity value predict that light was insufficient during this 6-week period to allow log growth and bloom inception. It makes little difference whether $\langle I \rangle$ is calculated from the monthly mean extinction coefficients or from those based on weekly observations of the variable Secchi disk depth. The subcritical in situ light intensity was mainly a function of the low incident radiation during this period.

The poor growth thus predicted during this 6-week period is confirmed with

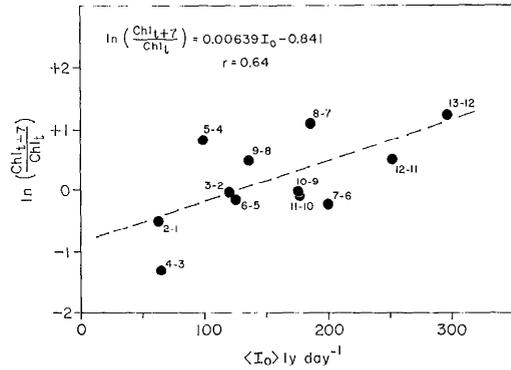


Fig. 2. Relationship between rate of increase in chlorophyll concentration over 7-day periods, from beginning (Chl_t) to end of week (Chl_{t+7}), and mean daily incident radiation for 7 days before sampling date ($t+7$). Numbers with data points identify weeks involved; data used are presented in Table 1.

chlorophyll *a* concentrations used as an index (Fig. 1). In mid-January (I) jumped suddenly to about 60 ly d^{-1} , and subsequently Riley's proposed critical intensity of 40 ly d^{-1} was usually exceeded. The vigorous phytoplankton growth accompanying the improved light conditions is clearly evident.

A positive correlation might be expected between the concentration of chlorophyll and the average incident radiation for several days before the sampling date, if increasing light intensity caused initiation of the 1972-1973 bloom. Following Riley's (1967) approach, we assume the rate of increase of the phytoplankton population (chlorophyll) to be equal to the rate of photosynthesis minus losses due to respiration, grazing, sinking, and advection:

$$\ln \frac{\text{Chl}_{t+7}}{\text{Chl}_t} = f(I_0) - \text{losses.}$$

It is further assumed that the losses are constant in the period involved and that growth is proportional to I_0 . Chl_t is the initial chlorophyll content, Chl_{t+7} that measured 7 days later, and I_0 is the mean incident radiation for 7 days before the sampling date ($t+7$). The data given in Table 1 were used.

Figure 2 demonstrates that in general the chlorophyll growth rate constant for a given week was dependent on the mean daily incident radiation during that week. The coefficient of correlation of 0.64 was significant at the 95% level. (A poorer correlation was obtained if the mean intensity for 3 days before $t+7$ was used.) This result strengthens the conclusion that light regulated bloom inception during 1972-1973.

Smayda (1973) suggested a critical incident radiation level of 0.10 ly min^{-1} at temperatures below 5°C and 0.05 ly min^{-1} between 5° to 10°C for the Narragansett Bay winter-spring bloom, based on the light-temperature growth response of *S. costatum* when incubated in bottles in situ. During December 1972, when the temperature ranged from about 4° - 6.5°C , this proposed level (Table 1) was nearly equalled or exceeded (ranged from 0.04 - 0.10 ly min^{-1}). Therefore, if light did have a major influence on the time of bloom initiation in 1972-1973, Smayda's suggested value should probably be raised by a factor of 2 or 3 when applied to natural populations of *Skeletonema* subjected to sinking, grazing, and advective losses.

Grazing losses would appear to be minimal during the prebloom period and not to account for the delayed bloom. Total zooplankton biomass (No. 10 net) ranged from 12.2 - 29.7 mg m^{-3} in December through mid-January (Table 1). The adult *Acartia clausi* population present during January through February was only 2 animals liter $^{-1}$ (Hulsizer 1976). At the prevailing temperatures and low population levels of *Skeletonema* then, a total daily grazing of 400 - $1,000$ cells liter $^{-1}$ is calculated from figure 8B in Smayda 1973. Even at the estimated December growth rate of 1 doubling per day, daily predation would take only a small percentage of the *Skeletonema* stock. The decline in population through December (Fig. 1) might have resulted from advective losses, even though a hydrodynamic model of circulation in Narragansett Bay (Kremer 1975) based on Hess and White's (1974)

numerical model suggests that the residence time of a particle at the sampling station is relatively long.

In summary, our study indicates that phytoplankton growth in Narragansett Bay during December 1972 through mid-January 1973 was greatly influenced by the available light. This contrasts with observations during previous years which suggest that a relaxation in grazing pressure determined the date of bloom inception. Although light may have little influence during most years, the present results indicate the need to include a light term in any model of bloom inception for shallow, well mixed Narragansett Bay. Additional experimental observations are needed to determine the critical incident and in situ light intensities for bloom inception in local waters. As a first approximation, Riley's (1967) value of 40 ly d^{-1} appears appropriate for the in situ critical intensity. It must be emphasized that this intensity is not a physiological constant, rather it is the point at which in situ phytoplankton growth exceeds losses.

It is of considerable interest that inception of spring blooms in Hood Canal, Washington (Barlow 1958), and off the Dutch coast (Gieskes and Kraay 1975) was also delayed until Riley's critical intensity of about 40 ly d^{-1} was attained.

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Submitted: 28 January 1975

Accepted: 2 August 1976