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EXPERIMENTAL OBSERVATIONS ON THE INFLUENCE OF TEMPERATURE, LIGHT, AND SALINITY ON CELL DIVISION OF THE MARINE DIATOM, *DETONULA CONFERVACEA* (CLEVE) GRAN[1,2]

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SUMMARY

The influence of 116 combinations of temperature (2, 7, 12, 16 C), salinity (5–35‰ at 5‰ intervals) and light (5 levels) on the mean daily cell division rate (K) *of the Narragansett Bay clone of* Detonula confervacea *was examined following appropriate preconditioning. Growth did not occur at 16 C, but was excellent (* K = *1.2–1.5) under certain combinations of light and salinity at 2, 7, and 12 C, being somewhat better at the 2 highest temperature levels. At 32‰ and 1100–1200 ft-c,* K *increased approximately 2.5-fold from 0.6 to 1.5 between 2 and 12 C.*

A light-temperature relationship was found which had the general trend of an increased optimal light intensity with increasing temperature. Within the optimal salinity range of 15–30‰, the optimal light intensity was 200–600 ft-c at 2 C, 600–1200 ft-c at 7 C, and 1200–1800 ft-c at 12 C. The light-temperature relationship was most pronounced at 2 and 12 C. At 2 C, K *decreased with increasing light intensity, but was independent of this factor at higher temperatures. The optimal salinity range of 15–30‰ was independent of temperature; negligible growth occurred at 5‰.*

In situ *and* in vitro *responses of* Detonula confervacea *to salinity were in general agreement; but its pronounced cryophilic preference in nature (usually reaching maximum abundance below 1 C) contrasts with its excellent growth at 12 C in culture. The experiments suggest that termination of the bloom of* Detonula confervacea *in Narragansett Bay and elsewhere is not solely temperature-dependent. Temperature does not satisfactorily account for its apparent exclusion from waters contiguous to Narragansett Bay and from other more northerly portions of the northeastern coast of the U.S., or, together with light, for its equally surprising apparent unimportance in Norwegian coastal waters.*

INTRODUCTION

The marine centric diatom, *Detonula confervacea* (Cleve) Gran, is an arctic species (***21***) which produces 2 or more resting spores per cell (***20***). Grøntved & Seidenfaden (***21***), who found it in abundance in net tows near West Greenland at approximately 76°N when the temperature ranged between –0.9 and –0.3 C, summarized the characteristics of its distribution and seasonal occurrence known as of 1937. Bursa's (***11***) annual survey near Igloolik Island (located near Baffin Island at about 70°N, 82°E), where *Detonula confervacea* was a major species, further illustrates its arctic character. It was first observed in mid-May under an ice layer 1.5 m thick in the upper 25 m at temperatures from –1.71 to –1.67 C; the maximum population[3] was then 21,540 cells/liter at 25 m. It persisted during the ensuing ice-free months, reached a maximum of 108,000 cells/liter in early August at 25 m and –0.86 C, and disappeared several weeks later. Thus, this species was always observed there below 0 C; the temperature during its occurrence ranged from –1.72 to –0.42 C.

Significant growth of *Detonula confervacea* under ice occurred in Isefjord, Denmark (***40***), although maximum populations (2×10^6 cells/liter) developed after melting. Curiously, it was not observed during the ice-free year of 1943 in this 3-year study. Observations in another Danish fjord (***30,22***) and in Narragansett Bay (***32,33***) demonstrate, however, that the growth cycle of *Detonula confervacea* is not dependent on a winter ice cover.

The distribution and regional and seasonal variations in abundance of *Detonula confervacea* are puzzling. It is conspicuously unimportant in Norwegian coastal waters (***5,8,9,14,16–18***), at least up to 70°N (***15***), notwithstanding the general occurrence of temperature, salinity, and light conditions similar to those accompanying its abundance in certain Danish fjords and in polar coastal waters (***3,11,21***). The maximum of 82,000 cells/liter reported from Oslofjord (***25***) is unusually high for these waters. Similarly, *Detonula confervacea* is apparently an unimportant early *summer* form in the Gulf of Maine (***1,3,19***); the maximum reported abundance is about 13,000 cells/liter at 9.5 C (***19***). It has not been reported from more southerly coastal waters along the eastern North American coast near Woods Hole (***13,29,26***) nor in Block Island (***34***)

[1] *Received December 5, 1968; revised January 21, 1969.*

[2] I wish to dedicate this paper to the memory of the recently deceased Julius Grøntved of the Danish Institute for Fisheries and Marine Research in recognition of his studies on *Detonula confervacea* and his contributions to our knowledge of phytoplankton and benthic diatom ecology, in general.

[3] Abundance values were obtained from the phytoplankton tables prepared by Bursa which were not included in his published article, but distributed by him in stencil form.

TABLE 1. *Maximum weekly (I = first week, II = second week, etc.) abundance (a) of* Detonula confervacea, *as cells ml⁻¹, and accompanying surface temperature (b), as C, in Narragansett Bay, Rhode Island, during the period of its occurrence from 1959 to 1967.*

Year:	1959		1959–60		1960–61		1961–62		1962–63		1963–64		1964–65		1965–66		1966–67	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
December																		
II															54	4.7		
III	–	–	11	5.0			36	3.1	1,539	2.8					92	3.9		
IV	–	–	0	3.8	9	1.2	559	2.0							35	3.3	0	2.2
V	–	–	0	4.0	–	–												
January																		
I	–	–	0	3.8	248	1.4	1,521	1.2	214	-0.6	8	–	0	2.5	2,240	3.2	0	1.8
II	–	–	0	1.0	654	1.2	3,666	2.4	222	0.6	100	–	0	2.2	117*	2.2	146	2.3
III	11,600	-0.6	10	2.1	814	2.0	2,197	2.1	1,356	1.2	210	1.2	0	-0.3	773	1.1	2,100	2.5
IV	5,661	–	19	2.6	2,920	–	5,800*	1.9	1,114	1.4	1,807	–	2	-1.1	2,400	0.3	6,700	2.5
V	–	–	–	–	4,160	0.8	8,580	1.8	884	-1.0	6,960	1.4	–	–	–	–	995*	2.4
February																		
I	2,169	-0.4	136	2.8	–	–	7,330	2.0	550	-1.0	8,780	0.9	37	-0.7	0	-1.0	43	2.8
II	2,460	-0.2	645	2.8	1,014	0.5	5,540	0	757	0.1	1,200	0.2	838	-0.2	0	1.0	80	0.9
III	3,380	0.6	2,961	2.4	–	–	3,042	0.6	1,260	-0.8	2,184	0.9	2,400	0.5	0	0.2	1,235	0.4
IV	2,448	0	1,950	3.0	793	3.4	3,042	1.0	3,550	-0.6	40	1.6	13,300	-0.3	1,600	1.0	56	0.4
March																		
I	1,830	1.2	1,222*	3.4	1,764	3.2	–	–	4,446	0.6	28	2.7	5,500*	0.4	732	2.8	402	0.2
II	1,566	2.2	585	2.6	2,987*	2.2	468	2.2	676	1.8	120	2.4	3,000	2.6	416	2.8	–	–
III	474	2.6	464	1.8	2,090	1.8	144	3.4	312	2.8	70	3.0	628	2.8	286	3.5	332	1.0
IV	852	3.2	1,196	2.8	2,284	4.4	0	3.9	329	3.6	118	4.3	60	2.4	0	4.5	0	2.5
V	695	3.8	553	3.2	–	–	–	–	–	–	–	–	244	3.1	–	–	–	–
April																		
I	630	5.8	1,326	6.4	160	3.9	22	6.9	399	6.9	26	4.2	188	3.7	78	4.5	0	5.9
II	360	6.7	1,170	5.5	273	5.1	0	8.2	0	6.3	24	5.8	152	5.5	142	6.1		
III	243	7.6	24	7.9	108	6.0	39	6.3			0	7.0	0	6.4	0	6.9		
IV	228	9.2	114	9.6	265	9.0	0	8.1			80	7.8	0	7.6	0	7.8		
V	–	–	–	–	–	–	–	–			0	8.9						
May																		
I	0	10.2	0	9.9	31	8.4					0	11.5						
II					0	9.6												

Symbols: no observations (–); resting spores abundant (*); see text for further explanation.

and Long Island Sounds (***12,35***). [Guillard & Ryther (***24***), however, report that it "has been present in the phytoplankton" of Moriches Bay, an embayment of Long Island Sound, in winter.] Yet in Narragansett Bay (41°30′N), which is contiguous with the latter 2 sounds, *Detonula confervacea* attains enormous abundance (Table 1) after initiating the annual winter-spring bloom (***32,33***). Its late February 1964 maximum of 13.3×10^6 cells/liter at –0.3 C considerably exceeds the densest populations apparently reported for it elsewhere in the literature.

Thus, 3 intriguing aspects of the natural behavior of *Detonula confervacea* are presently unexplainable: (1) the reasons for its considerable importance in Narragansett Bay (a temperate embayment), whereas other arctic species (***37,32,33***) are absent or quantitatively unimportant; (2) the reasons for its apparent absence in waters contiguous with Narragansett Bay; and (3) the causes of its apparent unimportance in seemingly suitable Norwegian coastal waters.

The seasonal and successional cycles of *Detonula confervacea* are also interesting. In Narragansett Bay (***32,33***) and in Danish waters (***40,22***), it initiates the winter-spring bloom with *Skeletonema costatum*, and is eventually replaced by it. In the polar waters separating Iceland from Greenland (Denmark Strait), *Detonula confervacea* is the character species of a late summer community, which includes dinoflagellates, and which Braarud (***3***) termed the "*Detonula*-vegetation." But rather than *initiating* the annual bloom, the "*Detonula*-vegetation" (maximum *Detonula confervacea* population of about 92,000 cells/liter at –0.50 C) was the fourth stage in a succession progressing from a green flagellate (under ice) to an *Achnanthes–Fragilaria* to a *Thalassiosira*–or *Chaetoceros* vegetation. Nutrients were approaching exhaustion during the *Detonula* stage. Thus, *Detonula confervacea* exhibits several different successional responses: bloom initiation in some boreal and temperate coastal waters, bloom termination in polar waters, and an intermediate response at Igloolik (***11***).

The few physiological studies on *Detonula confervacea* (all using a Narragansett Bay clone) can be summarized as follows: vitamin B_{12} is apparently not required (***23***); it exhibited equally good growth between 8–32‰, and a temperature optimum at 10 C,

TABLE 2. *Mean daily cell division rate* (K) *of* Detonula confervacea *grown at various combinations of light, salinity, and temperature (- represents no detectable growth).*

Salinity (‰):		5	10	15	20	25	30	35
Foot-candles	Temp (C)							
50	2	–	–	0.84	1.00	0.93	0.56	0.60
200	2	0.35	0.75	1.17	1.20	1.22	1.22	1.16
200	7	0.22	0.79	1.37	1.36	1.35	1.21	1.21
200	12	–	0.90	0.98	1.05	1.19	?	?
200	16[a]	–	–	–	–	–	–	–
600	2	0.27	0.87	1.01	1.11	1.10	1.06	1.06
600	7	0.56	0.93	1.37	1.50	1.52	1.59	1.28
600	12	–	0.72	0.97	0.96	0.99	0.92	0.67
1200	2	0.10	0.13	0.77	0.81	0.71	0.58	0.64
1200	7	0.26	0.90	1.20	1.47	1.43	1.30	0.94
1200	12	–	1.09	1.49	1.55	1.38	1.50	?
1800	2[b]	0.02	0.16	0.41	0.44	0.40	0.50	0.50
1800	7	–	1.05	1.19	1.41	1.40	1.25	0.97
1800	12	–	0.25	0.75	1.49	1.47	1.00	0.48

[a] No growth occurred at 16 C at these or any of the higher light-salinity combinations used.
[b] Cells chlorotic at all salinity conditions at this light-temperature combination.

with survival but no growth at 15 C (*24*); its respiratory coefficient (grams carbon respired/hour/gram chlorophyll) of 0.2–0.3 did not increase with temperature between 5 and 25 C following preconditioning at 5 and 10 C (*36*); poor growth relative to that with NO_3–N occurred with 5 organic N compounds, including urea and uric acid (*23*); and, finally, alkaline phosphatase production accompanies PO_4–P deprivation (*28*). Notwithstanding these observations, the physiological background for the intriguing regional and seasonal behavior of *Detonula confervacea* remains obscure. This, coupled with its numerical and successional importance in Narragansett Bay, led to the investigation reported herein.

METHODS

Detonula confervacea was isolated into unialgal culture from Narragansett Bay, Rhode Island (41°30'N). Stock and experimental cultures were grown in 50 ml of medium in 125-ml Erlenmeyer flasks under continuous "cool-white" fluorescent illumination. The medium at all times was filtered Narragansett Bay water enriched with Guillard's medium *f* (*23*).

Initial isolation was made into approximately 30‰ at 2 C and and 400–500 ft-c. Stock cultures were then established at 5, 10, 15, 20, 25, 30, and 35‰ through appropriate stepwise subculturing. Growth was feeble at 5‰ and several attempts were required to establish a 5‰ stock culture. Thus, *Detonula* was preadapted at each salinity used in the experiments for numerous transfers (at approximately weekly intervals). Growth of the 5‰ stock culture sometimes failed at the higher temperatures used; the inoculum was then taken from 10‰.

Preconditioning of stock cultures for at least one transfer was also carried out at or near the experimental temperature and light conditions used: 2, 7, and 12 C, and 50, 200, 600, 1200, and 1800 ft-c, respectively. Attempts to rear *Detonula* at 16 C at all light and salinity combinations were unsuccessful. The 50 ft-c illumination was used only in the 2 C series with several salinities. Experiments were run under 116 different combinations of light, temperature, and salinity (Table 2).

An inoculum giving about 400 cells/ml in the experimental flasks was taken from stock cultures in exponental growth grown at a preconditioning regime similar to the experimental conditions. The experiments for each temperature-salinity-light combination were run in triplicate. The experiments were terminated after 6-day growth by adding Lugol's preservative to the culture flasks. Cell numbers were then counted using a Palmer-Maloney chamber (*31*). The average number of cell divisions per day (*K*) for the 6-day growth period was calculated from

$$K = \ln \frac{C_t}{C_0} \left(\frac{1}{t \ln 2} \right)$$

where C_t and C_0 are cell concentrations at times t and 0, respectively, with C_t representing the mean terminal population of the 3 replicates.

RESULTS

The mean growth rates of *Detonula confervacea* at various combinations of temperature, salinity, and

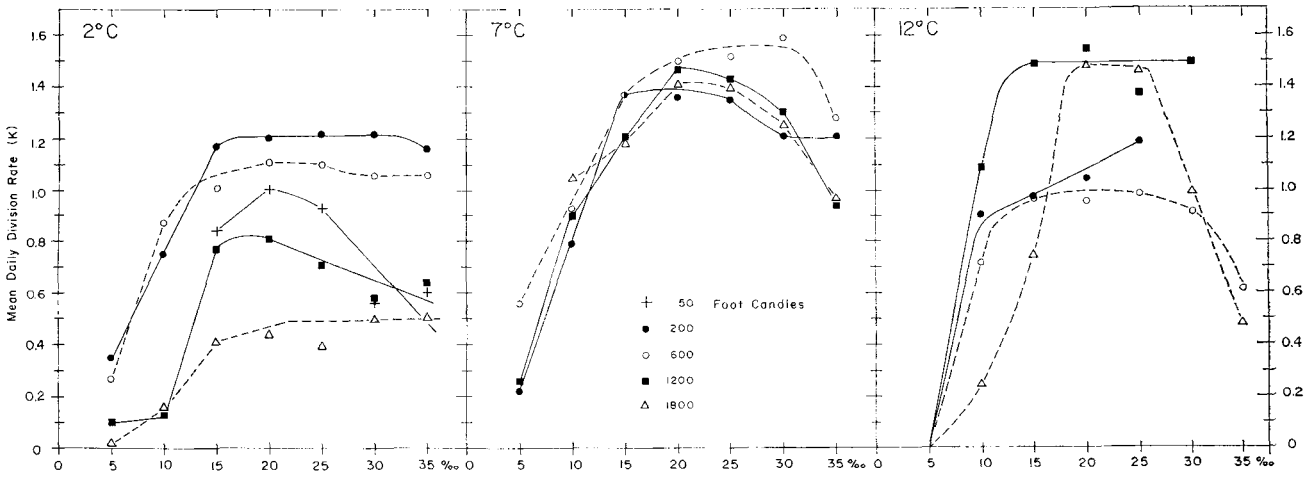

FIG. 1. The mean daily division rate of *Detonula confervacea* grown for 6 days at various combinations of light, temperature, and salinity, following preconditioning at these experimental conditions.

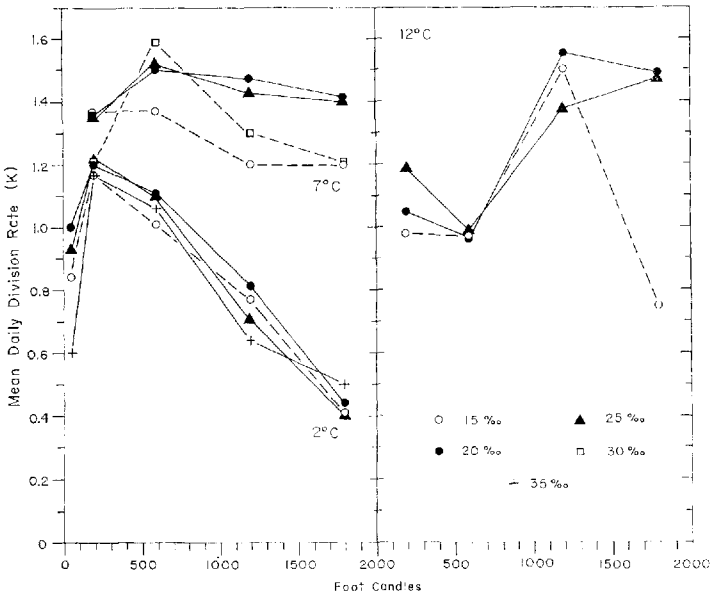

FIG. 2.

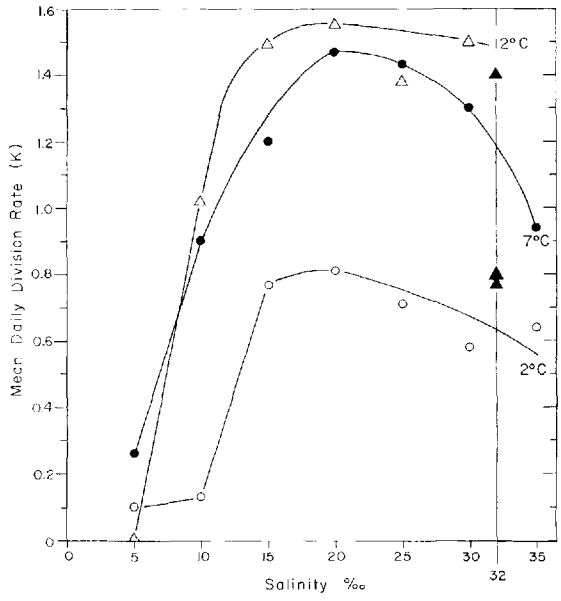

FIG. 3.

FIG. 2. The influence of light intensity on the mean daily division rate of *Detonula confervacea* grown at various temperature and salinity combinations.

FIG. 3. The mean daily division rate of *Detonula confervacea* grown at 1200 ft-c and various temperature and salinity combinations, and including results (▲) obtained by Guillard & Ryther [Fig. 3 (*24*)] using another clone of this species from Narragansett Bay and grown at 1100 ft-c, 32‰ and 4, 10, and 15 C.

light are presented in Table 2 and Fig. 1. Growth did not occur at 16 C, but was excellent under certain conditions at 12, 7, and 2 C. The maximum mean rate of about 1.5 cell divisions per day at the 2 highest temperatures exceeded that (1.25) at 2 C (Fig. 1). In general, better overall growth occurred at 7 C and, to a lesser extent, at 12 C than at 2 C for the various light-salinity combinations used (Fig. 1).

Growth was usually poor, when detectable, at 5‰ where a maximum mean rate of 0.56 division occurred at 7 C and 600 ft-c (Table 2). A rapid increase in cell division occurred up to 15‰ which generally remained more or less constant through 30‰, and declined at 35‰, irrespective of temperature.

There is a light-temperature relationship having the general trend of an increased optimal light intensity with increasing temperature (Table 2, Fig. 1, 2). Thus, within the optimal salinity range of 15–30‰ the optimal light intensity is 200–600 ft-c at 2 C, 600–1200 ft-c at 7 C, and 1200–1800 ft-c at 12 C. The light-temperature relationship was most pronounced at 2 and 12 C (Fig. 1).

Holding temperature constant at 2 C, the mean division rate *decreased* significantly with increasing light intensity between 15–35‰ (Fig. 2). Thus, the mean rate of 1.2 divisions per day at 20‰ and 200 ft-c exceeds that ($K = 0.44$) at 1800 ft-c by about 2.5-fold. Growth appeared to be light-limited at 50 ft-c at 2 C, the mean division rates approximating those obtained with the light inhibiting intensity of 1200 ft-c. An inverse relationship between light intensity and mean cell division was not found at 7 and 12 C. The mean division rate remained fairly constant at 7 C over the light intensity range, and within the salinity range of 15–25‰. Where the data permit an evaluation of the 12 C response, a less defined pattern is evident (Fig. 2).

Guillard & Ryther (*24*) determined the mean growth rate (from turbidimetric readings using a spectrophotometer) of an axenic Narragansett Bay clone of acclimatized *Detonula confervacea* over a 3-day period at 4, 10, and 15 C at 1100 ft-c and 32‰. (The salinity level was obtained by diluting Sargasso Sea water enriched with Guillard's medium *f*.) These results are plotted together with those obtained by me at 1200 ft-c for the various temperature-salinity combinations used (Fig. 3). The response of *Detonula confervacea* in the latter set was then interpolated for 32‰ in order to compare more effectively the available data from these 2 investigations in assessing the temperature response of this species. Figure 4 illustrates the influence of temperature on the mean daily division rate of *Detonula confervacea* grown at 32‰ and 1100–1200 ft-c. (While the interpolated values are, of course, influenced by the way the response curves are drawn in Fig. 3, the various possible curve trends do not appreciably influence the interpolated K value.) The growth rates found by Guillard & Ryther (*24*) at 4 and 10 C are consistent with the trend exhibited by the response at 2, 7, and 12 C interpolated for 32‰. Thus, at 32‰ and 1100–1200 ft-c the mean daily division rate increases approximately 2.5-fold from 0.6 to 1.5 between 2 and 12 C, i.e., $Q_{10} = 2.5$.

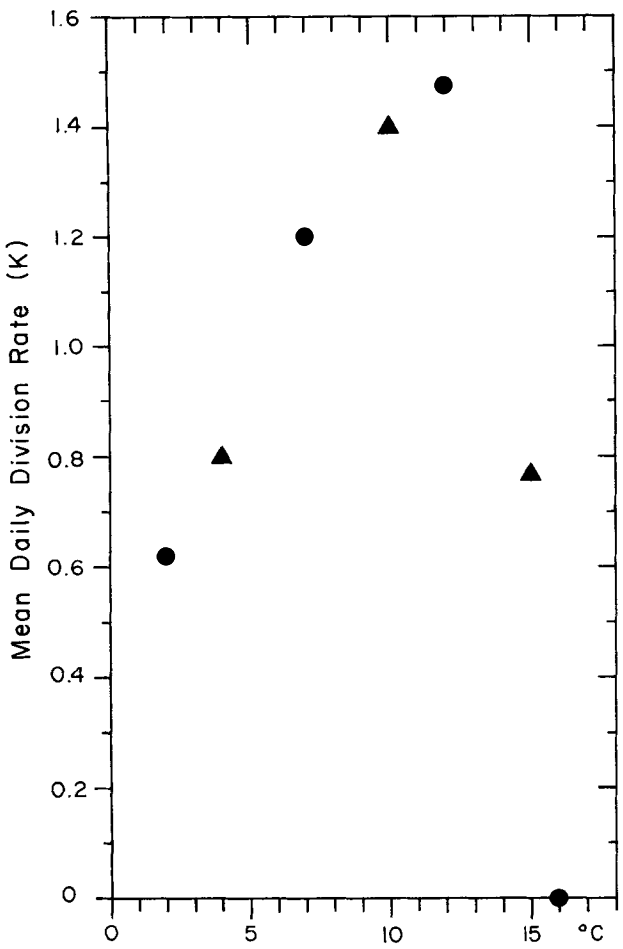

FIG. 4. The influence of temperature on the mean daily division rate of *Detonula confervacea* from Narragansett Bay grown at 32‰ and 1100–1200 ft-c. These data points taken from Fig. 3 at 32‰; the solid triangles (▲) represent Guillard & Ryther's (*24*) observations and the solid circles (●) represent the interpolated response at 32‰ based on the experiments described herein. See text for further information.

The temperature range bracketing the natural occurrence of *Detonula confervacea* seems to be –1.7 to 14 C (*11,2*), with a reported abundance of about 21.5 $\times$ 10^3 and 1.3 $\times$ 10^3 cells/liter, respectively, at these extremes. The temperature conditions accompanying the *maximum* reported abundance of *Detonula confervacea* in various areas are presented in Table 3. Obviously, it is a pronounced cold water form, often reaching its maximum *below* 1 C, but at slightly higher temperatures in Norwegian coastal waters. Both the modest maximum reported from the Gulf of Maine and the high accompanying temperature are clearly exceptional. The response of *Detonula confervacea* in Narragansett Bay (Tables 1, 3), where maximum annual populations of about 11 $\times$ 10^6–13 $\times$ 10^6 cells/liter occurred at –0.6 and –0.3 C, respectively, especially reveals its cryophilic behavior in nature. Pratt's observations (Table 1) show that its annual winter maximum occurred at temperatures below 1 C (from –0.6 to 0.9 C) during 6 of 9 consecutive annual cycles. The annual maximum occurred at 2–2.5 C during the remaining years. *Detonula confervacea* usually remains a dominant member of the Narragansett Bay phytoplankton community until surface temperatures exceed 5 C (*32*). In April 1960 significant populations persisted at 5.5–6.5 C; but in general *Detonula* seems to decline progressively at temperatures above 5 C, with remnants of waning populations remaining at 9–10 C.

DISCUSSION

Guillard & Ryther (*24*) previously found that acclimatized *Detonula confervacea* grew better (about 1.4 divisions per day) at 10 C than at 4 C, while cultures could not be maintained indefinitely above 15 C. They report that even the mean daily division rate of $K = 0.8$ at 15 C (Fig. 4) is somewhat misleading, since dead cells and resting spores were always present. Elsewhere, they report (*36*) inadequate growth at 15 C (unlike at lower temperatures) failed to provide sufficient material for respiratory measurements. These observations (also using a Narragansett Bay clone) are consistent with those reported here for 2, 7, 12, and 16 C. Collectively (Fig. 1–4, Table 2), they demonstrate that the mean daily cell division rate of *Detonula confervacea* increases significantly with temperature between 2 and 12 C, declines sharply at a temperature slightly higher than 12 C, and growth ceases at 16–17 C. The mean division rate at 10–12 C (Fig. 4) suggests that *Detonula confervacea* would fall into Group III of Braarud's (*5*) listing of diatoms based on their division rates at 10 C.

Where comparisons with previous studies (*24*) are possible, the observed salinity responses are also in general agreement.

These experimental results demonstrate that a con-

TABLE 3. *The maximum abundance and accompanying temperature observed for* Detonula confervacea *in various regions of its distributional range.*

Area	Cells/liter	Temp. (C)	Source
I. Norwegian Coast:			
a) Lofoten Islands (68°N)	4,280	3.5	(*14*)
b) Bergen (60°N)	480	4.2	(*16*)
c) Oslofjord (Drøbak, 59°N)	82,000	3.3	(*25*)
II. Danish Coast (~ 55–56°N):			
a) Limfjord	~ 900,000	0.9	(*22*)
b) Isefjord	2×10^6	0.7	(*40*)
III. "Greenland" Area:			
a) Denmark Strait (~ 65–67°N)	91,680	–0.5	(*3*)
b) Igloolik (69°N)	108,000	–0.9	(*11*)
IV. North American Coast:			
a) Bay of Fundy (45°N)	12,960	9.5	(*19*)
b) Narragansett Bay (41°N)	13.3×10^6	–0.3	Pratt (unpublished)

cise statement of the optimal growth requirements of *Detonula confervacea* cannot be made insofar as the light-temperature-salinity interactions are concerned. No particular combination of these factors permitted significantly better growth than any other, although certain combinations were clearly unsatisfactory. Given the type of preconditioning followed, and holding initial nutrients constant and at the levels used herein, the overall generalization emerges that the optimal temperature for cell division of *Detonula confervacea* is less than 15 C, while the optimal salinity is 15–30‰, irrespective of the light and tolerable temperature levels. Within this framework, the data (Fig. 1, Table 2) suggest the following general statements of optimal growth conditions for *Detonula confervacea*: (a) at 2 C, optimal growth occurs at 200–600 ft-c, and at 15–35‰; (b) at 7 C, optimal growth occurs at 200–1800 ft-c, and at 15–30‰; (c) at 12 C, optimal growth occurs at 1200 ft-c, at 15–30‰, and at 1800 ft-c at 20–25‰.

Braarud (*7*) discussed some of the problems involved in attempting to explain the dynamics of natural populations by applying the results of experimental autecological studies. It is still unknown to what extent a clone is representative of a local population, to what extent geographical clones exist, or how bacteria, whether by presence or absence, influence culture results. Therefore, the following attempt to account for the *in situ* regional and seasonal behavior of *Detonula confervacea*, as well as that in Narragansett Bay, from that found *in vitro* carries the above inherent limitations of such an approach. The following appraisal and conclusions are thus, at best, tentative.

Detonula confervacea has been found in nature at salinities ranging from about 10‰ (*22*) to 33.64‰ (*3*). Its great abundance in Narragansett Bay (Table 1) occurs at salinities of about 30–32‰. The poor growth of *Detonula confervacea* in culture at 5‰, when it occurs (Table 2, Fig. 1), is consistent with previous reports that it did not survive experimental salinities below 8‰ (*24*) and of its apparent absence from the Baltic Sea (*41*). The natural occurrence of 2×10^6 cells/liter at 19.76‰ (*40*), and a more modest abundance at 10–15‰ (*22*) are also consistent with the experimental results suggesting a salinity optimum from 15 to 30‰ (Fig. 1). Thus, cultured and natural populations of *Detonula confervacea* show reasonable, general agreement in their salinity response.

The excellent growth of *Detonula confervacea* at 12 C and its general temperature response in culture (Table 2) contrast sharply with its natural behavior which suggests optimal growth below approximately 2 C and feeble, if any, growth above 5 C (Tables 1, 3). In fact, the Narragansett Bay clones of this species have a greater thermal tolerance than might *a priori* be expected from its cold water behavior, or for cold water forms in general. Obviously, neither *Detonula*'s temperature response capability nor its biogeographic characterization could be adequately described based solely on these field observations or experimental results. A similar discrepancy between temperatures during natural abundance and growth in culture exists for the diatoms *Asterionella japonica* (*7*) and *Thalassiosira nordenskiøldii* (*4*). This sobering situation illustrates one of the potential pitfalls inherent in using physiological ecology and biogeographic extrapolations to account for phytoplankton behavior. The discrepancy between the *in vivo* and *in vitro* temperature responses for *Detonula confervacea* and *Thalassiosira nordenskiøldii* reflects that growth in culture is favored at temperatures distinctly higher than in their natural habitats. Bunt's (*10*) observations of a similar response by pennate diatoms isolated from Antarctic sea-ice now suggest that such differences between *in vivo* and *in vitro* behavior may be commonplace. Notwithstanding the reasons for this, including the possibility of inadequate experimental technique, certain biogeographic conclusions about *Detonula confervacea* seem valid. Namely, its growth at 12 C suggests that the termination of its bloom in Narragansett Bay, and its eventual elimination from the winter-spring community, are *not* temperature-dependent (Table 1). Further, temperature alone cannot satisfactorily account for its postbloom disappearance in other areas (Table 3), its surprising unimportance in Norwegian coastal waters, or its unexpected absence along much of the northeastern coast of the United States.

In Narragansett Bay *Detonula confervacea* has 2 pulses during most years (Table 1), although it is difficult to sift out the influence of water movements on these population changes. Significant resting spore formation (where such records were made by Pratt) often occurs in March, and as early as January at about 2–2.5 C (Table 1). In March 1965 spore formation was found even at 0.4 C; in 1960 it was 3.4 C. Therefore, this early development of resting spores suggests that postmaximal populations (especially above 5 C) are often waning, rather than growing during excessive predation, with patches at the highest temperatures in Narragansett Bay representing remnants of earlier populations. Elsewhere, ~ 40% of the March Oslofjord population (45,500 cells/liter) contained resting spores when the surface temperature was only 1.2 C (*25*). The growth experiments suggest, however, that temperature is not the primary environmental factor triggering resting spore formation in these particular instances. Spore formation in *Detonula confervacea* has been recorded in my stock cultures grown under continuous illumination of 400–500 ft-c at 2–3 C and 30‰. Guillard & Ryther (*24*) report that great numbers of resting spores were formed in nutrient deficient cultures and in those kept at temperatures close to the upper limit for

survival (i.e., 15 C). Thus, these observations also suggest, though indirectly, that temperature is not the primary determinant of the enigmatic seasonal and regional behavior of *Detonula confervacea*.

Figure 2 reveals 2 major light-temperature relationships which may influence the growth of *Detonula confervacea* in natural situations. At 2 C, which may be suboptimal in these particular experiments, an approximately 3-fold *decrease* in mean cell division rate accompanied increasing the light intensity from 200 to 1800 ft-c. At 7 C, however, growth ($K = \sim 1.4$) was *independent* of light level between the above extremes, suggesting that within certain limits *Detonula confervacea* requires a temperature increase to grow well at higher light intensities. The 2 C response does not appear to be unique to *Detonula confervacea*. Jitts *et al.* (**27**) reported that nonacclimatized *Thalassiosira nordenskiøldii* (a Narragansett Bay clone used) grew well in cold water only at low light intensities. Bunt (**10**) found the cell division of several Antarctic sea-ice diatoms to be inhibited at higher light intensities when grown at suboptimal temperatures. The chlorophyll content per cell in *Fragilaria sublinearis* grown at –2 C also decreased linearly with increased light intensity between 3 and 300 ft-c. The response (Fig. 2) of *Detonula confervacea* at 7 C (i.e., division independent of light intensity) also has certain parallels to the higher temperature-higher light response reported (**27**) for *Thalassiosira nordenskiøldii*.

Despite the use of different techniques, including light sources and species, these various observations are consistent in suggesting that within certain limits the influence of light on cell division is temperature dependent. This, coupled with our generally inadequate background knowledge of the influence of photoperiod, total intensity and adaptation on cell division, makes it difficult to apply the present results to natural situations. It is also still an open question whether the 2 C response of *Detonula confervacea* holds at even lower temperatures. Nonetheless, this response suggests that under certain conditions an increase in mean light intensity without a significant temperature rise may adversely affect cell division. It is unknown to what extent this situation influences *Detonula confervacea*'s cycle, particularly its demise, in Narragansett Bay and elsewhere. Since a temperature increase often reflects a gradual increase in light intensity, the successful transition from the 2 C to the 7 C type response appears to be primarily a problem of adaptation. It is unknown whether this is a factor leading to the unimportance of *Detonula confervacea* in Narragansett Bay at 5 C and at higher temperatures elsewhere (Table 1). The influence of light on its growth, however, suggests that this factor alone is not responsible for the apparent relative insignificance of *Detonula confervacea* in Norwegian coastal waters (**38**).

It is apparent that the general, natural behavior of *Detonula confervacea* cannot be satisfactorily explained by the results of these experiments. However, they do suggest that salinity and temperature are probably not important determinants of its behavior in Narragansett Bay, and that its apparent exclusion from or unimportance in certain areas are not primarily attributable to light, temperature or salinity, separately or in combination. At least, the present observations illustrate the type of factor interaction thought to be important in species succession (**39**). Obviously, the nutrient requirements of *Detonula confervacea* must be established next as part of this assessment. It is possible that *Detonula confervacea* is an example of Braarud's (**7**) view that a species requiring fairly high concentrations of nutrients might show a seasonal cycle similar to that of a cold water species.

NOTE IN PROOF

Crosby & Wood (1958, Studies on Australian and New Zealand diatoms. I. Planktonic and allied species. *Trans. Roy Soc. New Zealand* **85** (Pt. 4):483–530) reported *Detonula confervacea* as being: "oceanic, winter; a tropical form associated with the Coral Sea water mass." Should the existence of a tropical population of this species be confirmed, then the lack of growth of the Narragansett Bay clone at 16 C further suggests that the present experimental results cannot satisfactorily explain the general, natural behavior of *Detonula confervacea* throughout its range.

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