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The Physiological Ecology of a Marine Diatom, Skeletonema costatum (Grev.) Cleve[1]

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ABSTRACT

The marine plankton diatom, *Skeletonema costatum*, was isolated from local waters and cultured in enriched sea water. The effects of light, temperature, salinity, and concentrations of phosphorus and nitrogen on its growth and photosynthesis were determined separately and simultaneously. The effects of exocrine production by *Skeletonema* and grazing by copepods also were tested. The experimental results were used in developing an index of the photosynthetic potential of the diatom for seasonal hydrographic conditions found in the continental shelf waters south of Long Island.

Experimental results indicated that *Skeletonema* should have high photosynthetic rates and rapid cell division in late summer and early winter on the continental shelf by virtue of its responses to light and temperature alone. The usual concentrations of phosphorus and nitrogen on the shelf should not be limiting to this diatom.

The distribution and abundance of *Skeletonema* in 1956–1957 appeared to be in accord with predictions of potential photosynthesis except in offshore waters. Calculated photosynthetic rates and large standing crops occurred in late summer, decreasing toward late winter. The highest calculated photosynthetic rate in inshore waters was 29 % of the maximum rate, in July. The lowest calculated rates were for March through May.

Although the diatom ought to grow well offshore, it does not, apparently due to insufficient light during winter to support a stock for later growth. There is evidence that the lack of an undetermined nutrient also limits growth offshore.

Introduction. In natural phytoplankton populations, one algal species frequently predominates in numbers of individuals or in biomass. Such a situation may be taken as an indication of successful adaptation to prevailing environmental conditions, whether or not the species is an ecological dominant, in the sense of Shelford and Towler (1925). It should be possible to predict the physiological characteristics of an organism from its responses to the environ-

ment or, conversely, predict its responses in nature from physiological behavior in laboratory studies.

Frequently species that are important constituents of natural phytoplankton populations are singularly difficult to culture. However, *S. costatum* frequently is a major component of plankton blooms and grows extremely well in culture. It is present as far north as Thule, Greenland, and along the coast of the Gulf of Maine it is abundant and often "dominant" in summer and autumn (Bigelow 1926). It is the primary species in lower Narragansett Bay (Smayda 1957), Long Island Sound (Conover 1956) and Block Island Sound (Riley 1952), and has been very abundant in Chesapeake Bay (Cowles 1930) and at Beaufort, North Carolina (Manly 1953). In the Gulf of Mexico, it is abundant in spring and autumn though seldom if ever a primary species (Curl 1960). It seems to occur wherever plankton has been studied in coastal areas, except in the Arctic and Antarctic seas.

S. costatum was isolated in unialgal culture from Woods Hole Harbor in June 1957. Experiments were performed to study its responses to some of the chemical and physical variables important in local waters. Simultaneously, oceanographic cruises on the continental shelf south of Long Island yielded information on its distribution and abundance in natural populations, and associated hydrographic data. This paper correlates these laboratory and field observations.

Methods and Materials. Skeletonema was grown in enriched sea water (ESW), the composition of which is given in Table I. Sea water from Vineyard Sound, with an average salinity of 31°/oo, was filtered through a Millipore HA filter, enriched and autoclaved; its pH was 7.9–8.0 and its CO_2 concentration of 1.84 mmole; a five day supply of carbon at the maximum growth rates and cell concentrations used. The cultures were kept at 19–21°C under 10,000 lux illumination, and subcultures were made every fifth day. Rapidly growing cells, forming long chains, were used in the experiments.

TABLE I. Concentration of Enrichment Additives in ESW Medium (Formulated by J. H. Ryther).

Compound	Concentration	
	g/100 ml	mol. conc. μg–at/l
KNO_3	0.01	1000 NO_3–N
$Na_2HPO_4 \cdot 12 H_2O$	0.002	50 PO_4–P
$Na_2SiO_3 \cdot 9 H_2O$	0.0005	–
$Na_2S_2O_3$	0.00012	–
Ferric citrate	0.0003	–
Citric acid	0.0003	–
Vitamin B_{12}	0.12	–
Soil extract	0.5	–

Photosynthesis was measured by uptake of C^{14} according to the method of Steeman Nielsen (1952) as modified by Ryther (1954). The rates are expressed relative to the maximum value obtained in an entire series of experiments. The photosynthetic rate was determined after the cells had been exposed to the experimental conditions for periods which in different experiments lasted five or more days. The rates are therefore representative of the final experimental conditions in the culture.

RESULTS

Salinity. The effect of salinity on the rate of photosynthesis was studied in the range from 5–45°/oo. The Vineyard Sound sea water (31°/oo) was diluted with distilled water to give more dilute solutions; dried salt from local sea water was added to give higher concentrations.

Photosynthesis experiments, made one week after inoculation, showed the highest photosynthetic rates per cell at 15°/oo (Fig. 1). Considerable tolerance to higher salinities was evident. Throughout the salinity range of 11–40°/oo the rate of photosynthesis was at least half that of the maximum. When the salinity of the sea water was adjusted without adding nutrients, maximum photosynthesis occurred at 20°/oo. Both salinity and nutrients were diluted in the unenriched experiments, which may explain the lack of photosynthesis below 10°/oo. Carbon dioxide should not have been limiting at this concentration since 0.63 mmole/l was present initially.

Light and Temperature. Photosynthesis by cultures of *Skeletonema* in logarithmic growth phase was measured at temperatures from 5–30°C at light intensities varying from 0 to 36,000 lux. The incident light was attenuated
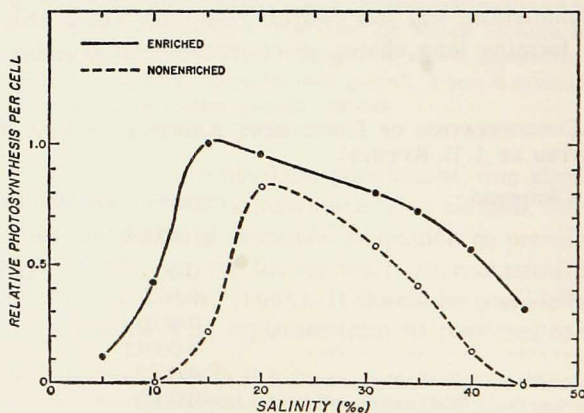

Figure 1. Relative photosynthesis in enriched and nonenriched sea water of varying salinities.
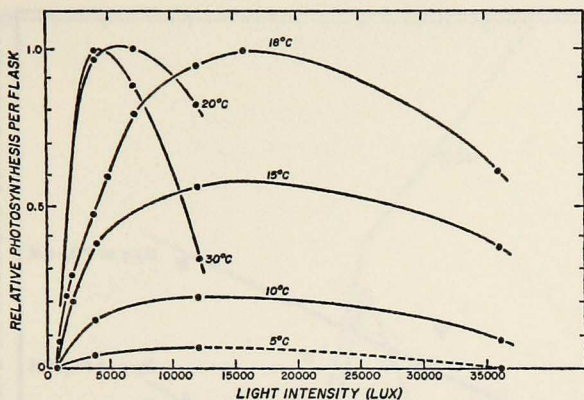
Figure 2. Relative photosynthesis as a function of light intensity at various temperatures.

with flat spectral distribution, neutral density filters. Replicates did not vary by more than 10%; averages are plotted in Fig. 2. The point at which apparent zero photosynthesis occurs is the compensation intensity. In these experiments all of the curves can be extrapolated to a compensation intensity of about 1,000 lux.

At temperatures ranging 5–18°C, light saturation occurred at 12,000 to 16,000 lux. Below 18°C the rates decreased with temperature, but light saturation still occurred from 12,000 to 16,000 lux. Above 18°C the saturation intensity was reduced to 4,000–6,000 lux, and the range in which maximum relative photosynthesis took place became very narrow. The decrease in photosynthesis at high light and temperature may be a result of greatly enhanced cell respiration. Matsue (1954) found that the highest temperature tolerated by *Skeletonema* was between 37° and 40°C.

Nutrients. Experiments were conducted to determine the effect of varying concentrations of phosphorus and nitrogen upon photosynthetic ability. After a culture had passed the logarithmic phase of growth and the cells could be presumed to be deficient in nutrients, aliquots were inoculated into an ESW medium containing varying concentrations of phosphorus and nitrogen. After two days growth at 18°C and 8,000 lux, C^{14} was added and carbon uptake was measured at the end of two hours (Fig. 3). The rate of photosynthesis was higher with enrichment by either nitrogen or phosphorus concentration; for all phosphorus concentrations the increase in rate of photosynthesis as a function of nitrate increment was about equal. Since these experiments measured the "population" photosynthesis rates, the rates could increase with higher nutrient concentrations almost indefinitely as more biomass was produced. The scale of relative photosynthesis for the entire nutrient concentration
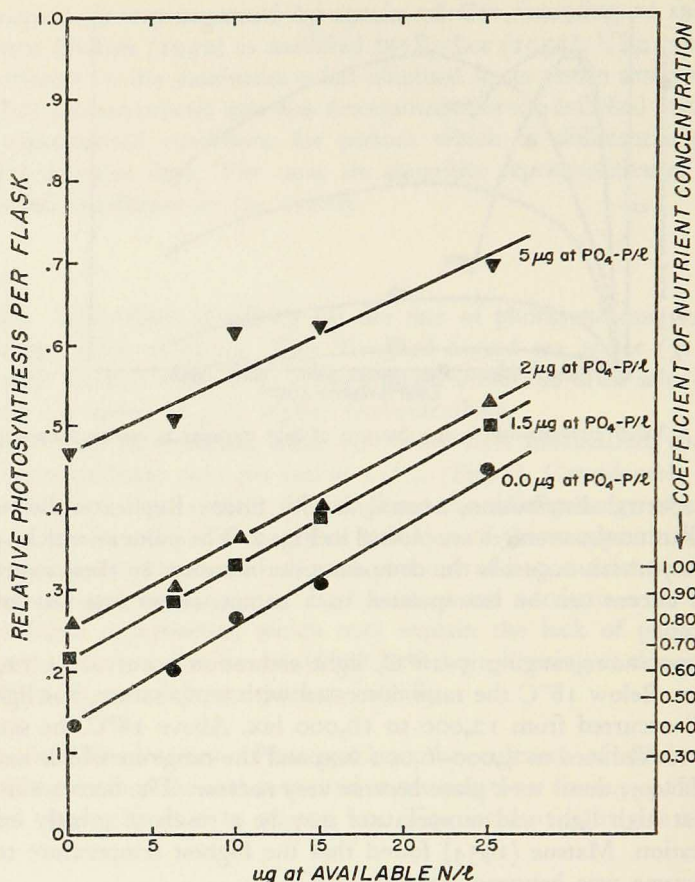
Figure 3. Relative photosynthesis as a function of low concentrations of phosphate phosphorus and available nitrogen. A scale of nutrient concentration coefficients replaces the scale of relative photosynthesis on the ordinate (see text).

range of the experiments has been discarded and a scale of nutrient concentration coefficients has been used in its place. The lower limit has been set at zero concentration. In order to have a coefficient of nutrient effect in the range 0–1.0, the upper limit has been set at the largest concentrations of phosphorus and nitrate that normally might be encountered in coastal Atlantic waters (0–1.0 μg-at available N/l, 0–1.5 μg-at PO$_4$–P/l) (Ketchum, *et al.* 1958).

Nutrients and Temperature. The effects of reduced amounts of nutrients on photosynthesis were studied at temperatures ranging from 5–30°C at a single light intensity (10,000 lux). Nitrate and phosphate were reduced to 0.1 the usual concentration, both separately and together. After inoculation from
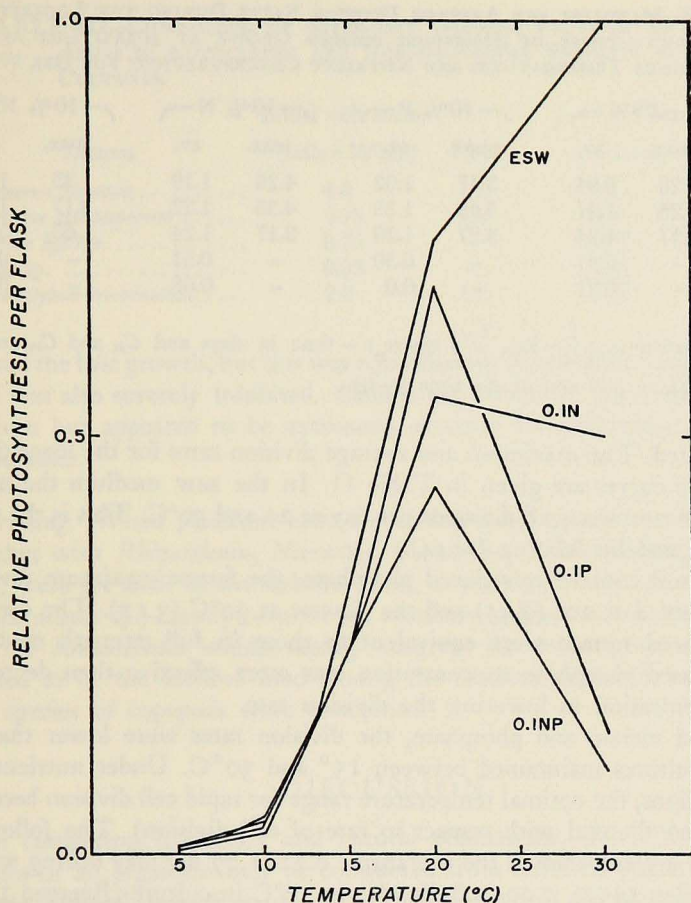
Figure 4. Relative photosynthesis as a function of temperature and nutrient concentration at 13,000 lux.

two-week old stock cultures, deficient in both phosphorus and nitrogen, the new cultures were equilibrated at the new temperature conditions for two days and then carbon fixation was measured for a two-hour period. Photosynthesis was at a maximum at 20°C at all nutrient dilutions (Fig. 4). The effect of reduced nitrogen alone was greater than reduced phosphorus at 20°C. The effect of reduced nutrients was greatest at the higher temperatures.

Studies of cell division rates at temperatures from 5–30°C were made at 13,000 lux in a complete medium and in a medium deficient in nutrients (Table II). Aliquots of a week-old culture growing in the ESW medium were inoculated into the ESW medium and into media deficient in nutrients, as used in the previous experiment. Cell counts were made daily until moribund

TABLE II. Maximum and Average Division Rates During the Logarithmic Growth-Phase of *Skeletonema costatum* Grown at 10,000 Lux and at Various Temperatures and Nutrient Concentrations for One Week*.

Medium	ESW		10% P		10% N		10% NP	
Temp. °C	max.	av.	max.	av.	max.	av.	max.	av.
30	4.28	0.94	3.17	1.02	4.25	1.19	1.35	1.05
20	4.28	1.21	3.45	1.35	4.35	1.22	3.17	1.24
15	3.17	1.24	3.27	1.28	3.17	1.24	1.66	0.89
10	–	0.47	–	0.50	–	0.51	–	0.51
5	–	0.21	–	0.0	–	0.08	–	0.01

* Division rate $k = \dfrac{1}{(t_2-t_1)} \log_2 \dfrac{C_{t2}}{C_{t1}}$, where t = time in days and C_{t1} and C_{t2} are cell counts at beginning and end of the time (t_2-t_1).

cells were noted. The maximum and average division rates for the logarithmic portion of the curves are given in Table II. In the ESW medium the maximum division rate was 4.28 divisions per day at 20 and 30°C. This is the same value determined by Matsue (1954).

In a medium containing reduced phosphate, the fastest maximum division rate was observed at 20° (3.45) and the slowest at 30°C (3.17). The division rates in reduced nitrate were equivalent to those in full strength medium. Thus, decreased phosphate concentration was more effective than decreased nitrate concentration in lowering the division rate.

In reduced nitrate and phosphate, the division rates were lower than in any of the cultures maintained between 15° and 30°C. Under nutrient deficient conditions, the optimal temperature range for rapid cell division becomes narrower (stenothermal with respect to rate of cell division). The following division rates are recorded in the literature: 0.21–1.77 div./day during winter in nature (Riley 1952), 0.90–2.6 div./day at 10°C in culture (Braarud 1937, 1945).

Exocrines. In order to determine whether *Skeletonema* produces substances affecting its own growth or that of other algae, several liters of a week-old culture were centrifuged and the supernatant millipore-filtered. The filtrate was re-enriched and half was autoclaved for half an hour. Subcultures using both autoclaved and nonautoclaved aliquots were inoculated with *S. costatum*, *Chaetoceros ceratosporum*, *Corethron hystrix*, *Ditylum* sp. and *Phaeodactylum tricornutum*. Cell counts were made after inoculation and again after seven days incubation at 18°C under 7,000 lux (Table III).

In the autoclaved medium, *Skeletonema*, *Ditylum* and *Phaeodactylum* made good growth, *Chaetoceros* perished and *Corethron* grew slowly. In the nonautoclaved medium, *Chaetoceros* and *Ditylum* grew not at all and *Corethron* and *Skeletonema* required seven days to double their numbers. *Phaeodactylum*

TABLE III. COMPARISON OF SEVEN-DAY GROWTH RATES AT 18°C, 7,000 LUX; ALGAE IN AUTOCLAVED AND NONAUTOCLAVED FILTRATE FROM *Skeletonema* CULTURES.

Diatom	Initial cell count (cells × 10⁴/ml)	ESW	— Division per day — autoclaved	nonautoclaved
Skeletonema costatum	4.0	1.2	1.1	0.04
Chaetoceros ceratosporum	0.75	1.0	0.0	0.00
Corethron hystrix.............	0.25	–	0.57	0.12
Ditylum sp.	0.03	–	0.81	0.00
Phaeodactylum tricornutum	2.2	1.0	1.0	0.60

showed the best growth, but this was equivalent to only 0.6 div./day. *Skeletonema* itself was also severely inhibited. *Chaetoceros* ordinarily grew well in an ESW medium but appeared to be extremely sensitive to substance(s) produced by *Skeletonema*.

Grazing. When plankton tows containing large quantities of *Skeletonema*, together with *Rhizosolenia, Nitzschia, Guinardia, Thalassionema,* and *Chaetoceros*, were set aside in the culture room, copepods (mainly *Acartia tonsa* and *Pseudocalanus* sp.) rapidly reduced the numbers of *Skeletonema*, leaving uneaten cells of *Rhizosolenia* which rapidly outgrew the other genera. *Skeletonema* seemed to be the favored food among the diatoms available, so far as these two species of copepods were concerned.

DISCUSSION

In comparing laboratory and natural populations, the environmental responses of an organism may be considered from different points of reference. In one, optimal growth conditions are determined in the laboratory and then similar conditions are sought in nature. Large populations would tend to occur where such conditions were found, and smaller populations elsewhere. However, the environmental and physiological conditions of the organism are changing with time. Riley, *et al.* (1949) attempted a prediction of productivity in nature based on laboratory results, taking these changing conditions into account by substituting into a differential equation.

Here an attempt is made to evaluate the potential productivity of *Skeletonema* on the continental shelf, on the basis of laboratory results, by determining the photosynthetic rates under the physical and chemical conditions obtaining at monthly intervals throughout the year. The potential or "predicted" productivity rates may be compared with the actual abundance and distribution of the populations in nature.

In our experiments, light and temperature were factors that interacted in such a way that they should be considered simultaneously. Salinity and the

concentrations of available nutrients affect the photosynthetic rate, and the initial concentrations of phosphate and nitrate determine the size of the standing crop. *Skeletonema* inhibits its own growth when grown in dense cultures. Finally, the alga is consumed readily by some copepods.

To obtain data for natural conditions, the effects of salinity, light, temperature and nutrients on the potential photosynthesis of *Skeletonema* have been evaluated for the coastal waters south of Long Island, where observations were made during six cruises between September 1956 and September 1957. The data for adjoining stations have been combined and averaged over the depth of the wind-mixed layer, as determined by the pycnocline. This has been done separately for three depth ranges, *i. e.*, stations in water less than 100 m deep, between 100 and 500 m, and over 500 m. Values for months during which no observations were available were interpolated from smoothed seasonal curves.

For each group of stations the combined effect of light and temperature (Fig. 2) was determined as a per cent of the maximum photosynthesis obtained in the experiments (relative photosynthesis). Subsequently, the separate effects of salinity (Fig. 1) and of phosphate and nitrate (Fig. 3) were evaluated; the cumulative effects given by the product of each successive factor provided the potential productivity.

The average light intensity in the mixed layer was derived from the formula of Riley (1957), using Kimbal's (1928) tables. These data were reduced by 50% to eliminate the energy from wavelengths not available for photosynthesis. They have been converted from energy to intensity units by the relationship: 1 g cal/cm²/min = 155×10^3 lux (Ryther 1956 b). The duration of daylight was taken from Baker (1938). Light attenuation coefficients were obtained either by secchi disc reading or by submarine photometer.

At the shallow stations (Table IV), on the basis of light and temperature alone, the highest potential photosynthetic rates occurred in July and September (72%) and the lowest in midwinter (3–7%). Introduction of the salinity effect decreases all monthly values without fundamental change in the pattern. The combined effect gives a maximum value of 57%, and a minimum of 2.3%. The nutrient effect further reduces these to 26% and 1.5%. The same analysis has been applied to the results from the "intermediate" and deep stations (Tables V and VI). The cumulative effect of all factors shows that during most of the year the potential photosynthetic rates were higher at the intermediate stations than inshore. The potential ranged from 3–32% at the intermediate stations. At the deep stations the potential rates ranged from zero in winter, when the mixed layer was very deep, to values as high as 29–34% in summer and autumn.

The standing crops of *Skeletonema* observed in this case are shown in Fig. 5. The large populations observed from September through February correspond with the calculated high potential photosynthesis rates for the beginning of

TABLE IV. THE FRACTIONS (P) OF MAXIMUM PHOTOSYNTHESIS COMPUTED SUCCESSIVELY FOR TEMPERATURE AND LIGHT (t, i), SALINITY (s) AND NUTRIENTS (n). THE CUMULATIVE EFFECT (POTENTIAL PHOTOSYNTHESIS) IS GIVEN BY THE PRODUCT OF THESE (Ptisn).

DATA FOR STATIONS WITH WATER DEPTH OF 100 M OR LESS.

Date†	Light (lux)	Temp (°C)	P_{ti} (%)	Salinity (%o)	P_s (%)	P_{tis} (%)	PO_4–P (μg-at/liter)	Avail.N	P_n (%)	P_{tisn} (%)	Calculated net C fixation (g/m²/day)	Per cent of total net photosynthesis	Net photo-synthesis (g/m²/day)*
Sept.	7560	17	72	31.9	80	57	0.34	0.82	46	26	.131	84	.156
Oct.	6200	15	48	32.5	78	37	0.55	1.7	54	20	–	–	–
Nov.	2860	14	27	33.1	77	21	0.62	2.0	56	12	–	–	–
Dec.	2300	12	16	33.1	77	12	0.62	3.6	64	8	.596	101	.557
Jan.	2720	8	7	33.2	76	5.3	0.75	3.5	65	3	–	–	–
Feb.	2410	5	3	33.2	76	2.3	0.74	3.35	62	1.5	.072	13	.550
Mar.	6180	6	7	33.0	76	5.3	0.60	2.22	58	3	.000	0	.109
Apr.	8330	6	8	33.1	77	6.2	0.60	1.7	57	4	–	–	–
May	8520	8	16	33.1	77	12	0.48	1.25	50	6	.000	0	.106
June	7880	13	38	32.8	78	30	0.45	1.7	52	15	–	–	–
July	7200	17	72	32.5	78	56	0.33	1.8	51	29	.101	2	.500
Aug.	7400	16	60	32.6	78	47	0.33	1.5	50	24	–	–	–
Sept.	7610	16	63	32.7	78	49	0.32	1.01	50	25	–	–	–

* Calculated from Ryther and Yentsch (1958).

† Underlined months are those for which hydrographic data are available. Others are extrapolated.

TABLE V. The Fractions (P) of Maximum Photosynthesis Computed Successively for Temperature and Light (t, i), Salinity (s), and Nutrients (n). The Cumulative Effect (Potential Photosynthesis) is Given by the Product of These (P_{tisn}).

DATA FOR STATIONS WITH WATER DEPTHS OF FROM 100 TO 500 M.

Date†	Light (lux)	Temp (°C)	P_{ti} (%)	Salinity (‰)	P_s (%)	P_{tis} (%)	PO_4–P (μg-at/liter)	Avail.N	P_n (%)	P_{tisn} (%)	Calculated net C fixation (g/m²/day)	Per cent of total net photosynthesis	Net photosynthesis (g/m²/day)*
Sept.	8060	19	92	34.6	74	68	0.12	0.94	45	31	.001	0.5	0.19
Oct.	6590	18	77	34.4	74	57	0.20	1.50	48	26	–	–	–
Nov.	2090	15	25	33.4	77	19	0.40	2.50	54	10	–	–	–
Dec.	1670	15	15	34.0	74	11	0.50	4.15	64	7	.012	2	0.52
Jan.	1980	12	11	34.3	74	8	0.62	5.2	68	5	–	–	–
Feb.	1890	9	7	34.2	74	5	0.62	6.1	74	5	.025	15	0.16
Mar.	2600	8	9	33.8	76	7	0.52	3.42	60	4	.000	0	1.60
Apr.	2180	9	9	34.0	74	7	0.62	2.8	45	3	–	–	–
May	2240	10	10	34.1	75	8	0.41	1.05	50	4	.000	0	0.71
June	4810	13	32	33.8	76	24	0.30	1.00	50	4	–	–	–
July	7450	16	61	33.5	77	47	0.25	0.94	46	21	.000	0	0.37
Aug.	7330	17	72	33.9	76	55	0.35	2.00	52	28	–	–	–
Sept.	7900	17	73	34.3	74	54	0.52	3.1	60	32	–	–	–

* Calculated from Ryther and Yentsch (1958).

† Underlined months are those for which hydrographic data are available. Others are extrapolated.

TABLE VI. THE FRACTIONS (P) OF MAXIMUM PHOTOSYNTHESIS COMPUTED SUCCESSIVELY FOR TEMPERATURE AND LIGHT (t, i), SALINITY (s) AND NUTRIENTS (n). THE CUMULATIVE EFFECT (POTENTIAL PHOTOSYNTHESIS) IS GIVEN BY THE PRODUCT OF THESE (P_{tisn}).

DATA FOR STATIONS WITH WATER DEPTH OF FROM 500 TO 2000 M.

Date†	Light (lux)	Temp (°C)	P_{ti} (%)	Salinity (‰)	P_s (%)	P_{tis} (%)	PO_4-P (µg-at/liter)	Avail.N (µg-at/liter)	P_n (%)	P_{tisn} (%)	Calculated net C fixation (g/m²/day)	Per cent of total net photosynthesis	Net photosynthesis (g/m²/day)*
Sept.	9230	23	88	35.6	73	64	0.13	0.55	45	29	0	0	0.21
Oct.	7550	21	97	35.5	72	70	0.20	1.00	47	33	–	–	–
Nov.	1090	18	17	35.0	75	13	0.30	2.00	52	7	–	–	–
Dec.	870	16	3	35.2	72	2	0.36	3.09	57	1.2	.000	0	0.18
Jan.	1040	14	15	35.4	72	11	0.53	5.6	72	8	–	–	–
Feb.	830	13	1	35.5	72	0.7	0.62	6.5	71	0.5	.000	0	0.10
Mar.	590	15	0	36.1	71	0	0.52	5.3	67	0	.000	0	0.56
Apr.	590	14	0	35.8	73	0	0.50	3.70	65	0	–	–	–
May	600	13	0	35.3	72	0	0.35	1.73	50	0	0	0	1.03
June	3950	17	45	35.2	72	32	0.25	1.00	47	15	–	–	–
July	7310	20	100	35.0	75	75	0.12	0.84	45	34	0	0	0.19
Aug.	5750	20	100	35.5	72	72	0.13	0.90	46	33	–	–	–
Sept.	4750	20	100	36.0	71	71	0.19	0.92	46	33	–	–	–

* Calculated from Ryther and Yentsch (1958).

† Underlined months are those for which hydrographic data are available. Others are extrapolated.
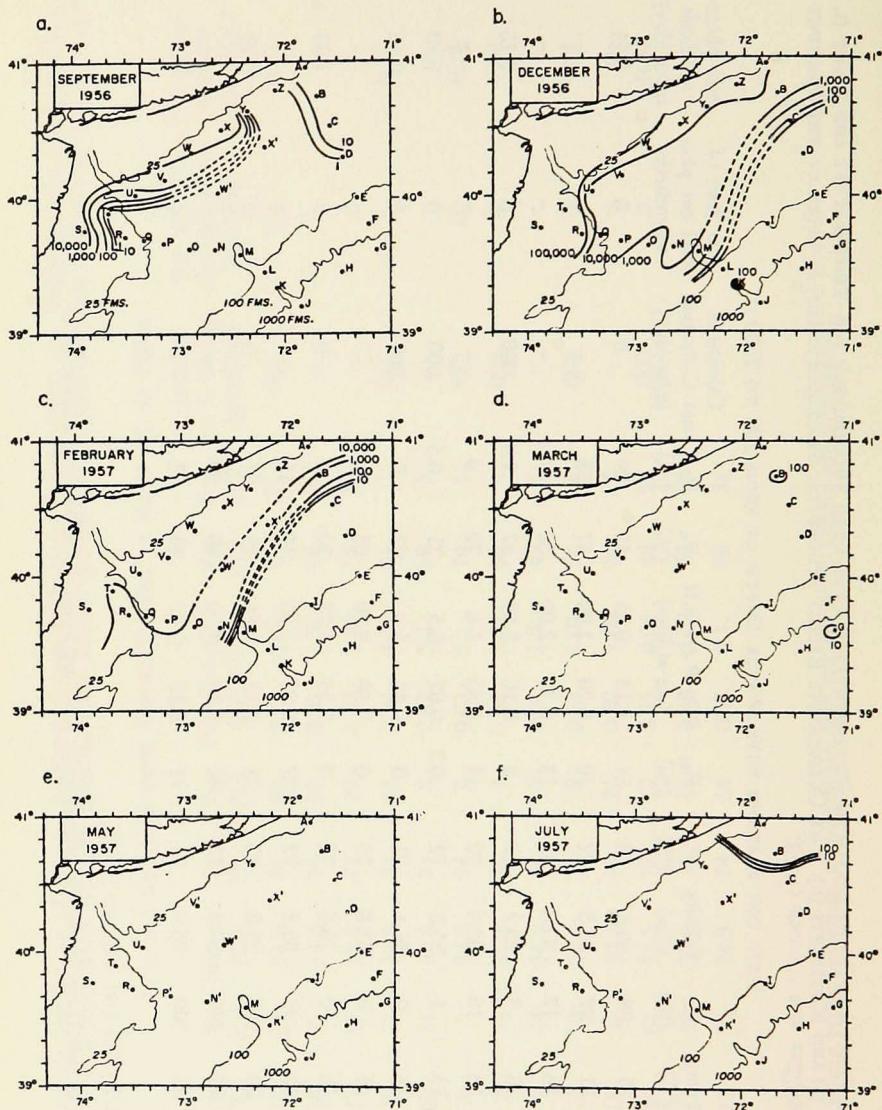
Figure 5 a–f. Distribution of *Skeletonema* (cells per liter) at 10 m depth on the continental shelf from September 1956 to July 1957.

this period. Likewise, the almost complete absence of cells from March onward corresponds with the calculated lack of photosynthesis by *Skeletonema* during this period. The appearance of a small bloom in July is in accordance with the prediction of an increase in *Skeletonema* photosynthesis in early summer (Table IV).

It would be ideal to be able to compare calculated potential photosynthesis with actually measured photosynthesis of the species, but only the total phytoplankton photosynthesis is available (last column, Tables IV, V, and VI).

For the shallow waters, at least, light and temperature appear to be the controlling influences on the seasonal appearance of *Skeletonema* whereas the size of the standing crop is controlled by an interaction of all the factors.

The fact that the population continues to increase from September through December may be explained by the supposition that the standing crop reflects a time lag between the environmental conditions and their expressions. Zooplankton grazing may be implicated also. Riley (1956) calculated that 65% of the phytoplankton produced in Long Island Sound was consumed by pelagic organisms. Our evidence indicates that *Skeletonema* is readily eaten by small copepods in "preference" to some other genera. Zooplankton volumes averaged 46% lower in the November-December cruise than in the September cruise. Volumes in February and March increased and were greatest in March (Curl, unpublished). Cladocera and copepods predominated in the samples. Grazing appears to be a plausible explanation of reduced cell numbers in September.

The intermediate and deep stations never supported large standing crops of *Skeletonema* despite good conditions for growth. Because zooplankton volumes were low at these stations, some factor not considered thus far must be limiting. Since the diatom is so obviously a neritic species, despite good growth conditions on the deep shelf, the factor (s) may be associated with proximity to either the benthos or land. *Skeletonema* requires both vitamin B_{12} (Droop 1955) and divalent sulfur (Lewin, personal communication), among other nutrients. The seaward advection, dilution by mixing, and biological destruction of such substances would make them unavailable to it on the deep shelf and would help to account for its observed spatial distribution.

Calculated zero potential photosynthesis at deep stations is indicative of deep mixing below the euphotic zone in winter (50% of the population may be below the compensation depth). However, when the thermocline is present, the potential photosynthetic rates are frequently more than double those close inshore. Nevertheless, *Skeletonema* is absent from offshore waters. One reason is that virtually no photosynthesis is possible during seven months of the year, and it has been shown that cells of *S. costatum* can survive only two months of darkness. Matsue (1954) found that *Skeletonema* could be kept in the dark up to 52 days without high mortality but that no cells survived beyond 60 days. Our experience agrees with this result. Moreover, if some substance derived

from land drainage is essential for growth, it is even less likely to be found at the deep stations.

The circulation out of the lighted zone in winter is a condition to which almost all oceanic algae are subjected. A necessary consequence is that oceanic species must be able to tolerate periods of low illumination.

The photosynthesis of observed natural populations of *Skeletonema* can be estimated from our data. The maximum carbon fixation per cell is known from laboratory experiments, and the potential fraction of this value for each month has been calculated. These multiplied by the average cell concentration give the estimated carbon fixation by *Skeletonema* in nature. The highest photosynthetic rate observed in the laboratory was 1.76×10^{-3} mg C/10^4 cells/hour, calculated from C^{14} uptake. (*Chlorella*, which has one of the highest photosynthetic rates known, has a maximum reported rate of 16×10^{-3} mg C/hr/μl cell volume [Hill and Whittingham 1957] whereas *Skeletonema* fixed 2.8×10^{-3} mg C/hr/μl cell volume in our experiments.) The net carbon fixation at each station may be derived from the formula:

(cells/m3) $\times (1.76 \times 10^{-7}$ mg C$) \times$ (hrs daylight) $\times$ (m depth) $\times$ (% max. photosynthesis) $=$ gC/m²/day.

The depth used in this calculation is that of the mixed layer as previously used. In tables V–VII these computed values are compared with the observed total phytoplankton net photosynthesis computed from the data of Ryther and Yentsch (1958). A maximum of 0.596 gC fixed/m²/day by *S. costatum* is calculated for December at the shallow stations. These rates correspond to 100% of the observed fixation for this area and time. *Skeletonema* also could have accounted for 84% of the carbon fixation in September 1956. During the period of greatest carbon fixation, in March and May, it was not present. The comparative absence of *S. costatum* cells at the intermediate and deep stations throughout the year accounts for their lack of contribution to the total phytoplankton production.

Thus far, data for the seasonal occurrence of *Skeletonema* for one year have been examined. From similar data from inshore waters in other years it may be determined if the distribution of 1956–1957 was typical. Cell counts of *Skeletonema* from Vineyard Sound 1950–1951, Woods Hole 1956–1957 (Hulburt, unpublished), Narragansett Bay 1954–1955 (Smayda 1957), Block Island Sound 1949 (Riley 1952), Vineyard Sound 1935 (Lillick 1937), and Long Island Sound 1952–1954 (Conover 1956), were averaged for each month of the year irrespective of year or geography. Although the actual counts range from 0 to 20×10^6 cells per liter at any one particular place and time, the averages plotted against time yield a smooth bimodal curve (Fig. 6). The outstanding difference between the postulated shelf pattern and the inshore observations is the bimodal nature of the latter. The late autumn and winter peak occurs on the shelf but lags behind the high summer potential.
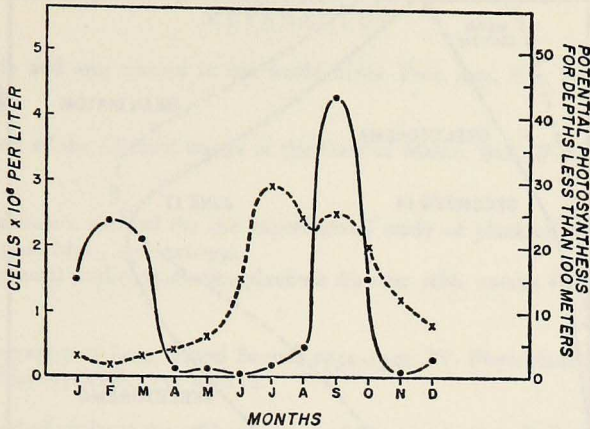
Figure 6. Averaged *Skeleotnema* concentrations in the inshore waters of the northeastern states, and calculated potential photosynthesis. Solid line, cell concentration; dashed line, potential photosynthesis.

A spring bloom of this species does not ordinarily occur in the self waters. For example, Bigelow (1926) says, this genus is ". . . closely confined to the immediate vicinity of the land in the Gulf of Maine and to the shallow water of the banks, where it flowers irregularly during summer and early autumn. . . In north European waters it has its maximum in spring but has been found flowering in autumn as well at many localities." The inshore spring flowering here and possibly the spring flowering in Europe must be a response to a factor not studied.

Conover (1956) and others have noted that *Thalassiosira nordenskioldii* Cl. occurs under nearly the same conditions as does *Skeletonema* and seems to be its closest competitor. The optima of light and temperature for the growth of *Skeletonema* are higher than those for *Thalassiosira*. Ryther (1956 a) derived an average relationship between light intensity and photosynthesis from studies of several species of diatoms, and a comparable curve has been derived for *Skeletonema* (Fig. 7). In the summertime *Skeletonema* tends to be favored by shade compared to the "average diatom" and would be inhibited at light intensities exceeding 25% of the surface value. If the mixed depth was as deep as the compensation depth or deeper, then *Skeletonema* would be able to equal the daily production of the "average diatom". In December, however, *Skeletonema* behaves like an "average diatom" at 12°C and can be significantly more productive than the average at 16°C. From a competitive viewpoint *Skeletonema* should fare best in early winter, and it certainly seems to do so.
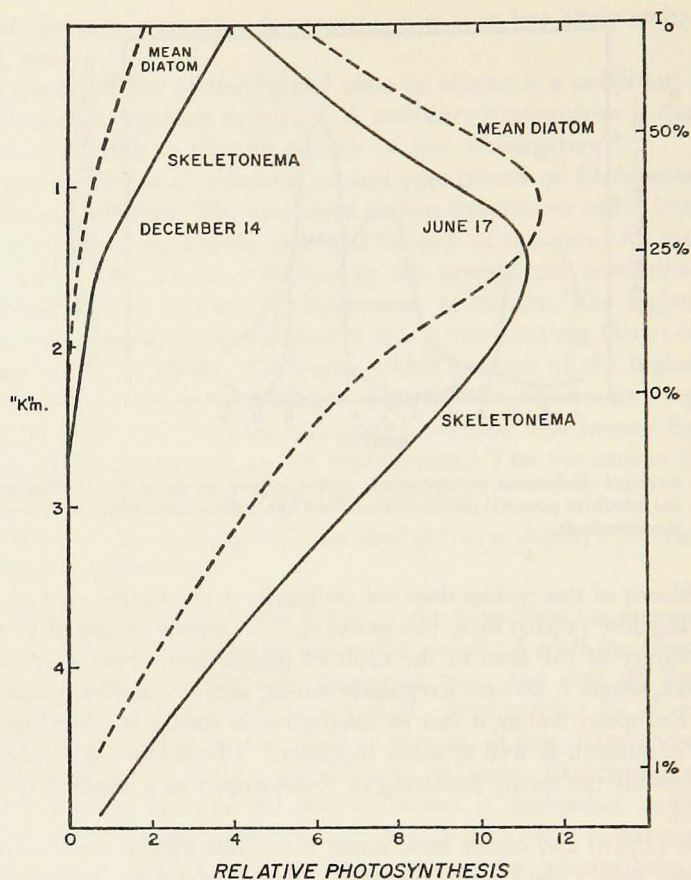
Figure 7. Integrated relative daily photosynthesis of *Skeletonema* as compared to that of the mean values for diatoms in general.

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