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Seasonal Studies on the Relative Importance of Different Size Fractions of Phytoplankton in Narragansett Bay (USA)

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Abstract

The composition and productivity of four different size-fractions (< 20, 20 to 60, 60 to 100, > 100 µm) of the phytoplankton of lower Narragansett Bay (USA) were followed over an annual cycle from November, 1972 to October, 1973. Diatoms dominated the population in the winter-spring bloom and in the fall; the summer population was dominated by flagellates. The nannoplankton (< 20 µm) were the most important, accounting for 46.6% of the annual biomass as chlorophyll *a* and 50.8% of the total production. The relative importance of the different fractions showed a marked seasonality. During the winter-spring and fall blooms the netplankton fractions (> 20 µm) were the most important. Nannoplankters dominated in the summer. The yearly mean assimilation numbers for the different fractions were not significantly different. During the winter-spring bloom, however, the assimilation numbers for the netplankters were significantly higher than those for the nannoplankton fraction. Temperature accounted for most of the variability in assimilation numbers; a marked nutrient stress was observed on only two occasions. Growth rates calculated from ^{14}C uptake and adenosine triphosphate (ATP)-cell carbon were generally quite high; maxima were > 1.90 doublings per day during blooms of a flagellate in the summer and of *Skeletonema costatum* in the fall. The series of short cycles observed in which the dominant species changed were related to changes in the physiological state of the population. Higher growth rates were generally observed at times of peak phytoplankton abundance while lower growth rates were observed between these peaks. The high growth rates and assimilation numbers usually found suggest that the phytoplankton in lower Narragansett Bay was not generally nutrient-limited between November, 1972 and October, 1973. Nutrient regeneration in this shallow estuary, therefore, must be very rapid when *in situ* nutrient levels are low.

Introduction

In the study of species succession in marine phytoplankton, floristic changes have traditionally been of primary concern. However, an understanding of the process of succession requires evaluation of the biological differences between species within the community (Smayda, 1973a). These biological differences will be reflected in differences in individual species' nutrient requirements and uptake kinetics, photosynthetic and respiration rates, sinking rates and in their suitability as food for grazers. Increasing evidence suggests that basic first-order differences in these factors among different species may be organized according to differences in cell size. Williams (1964) has shown that small cells have higher intrinsic growth rates. In nutrient-uptake kinetics, cell-suface to volume considerations predict that large-celled species are less able to absorb nutrients from low-nutrient waters (Munk and Riley, 1952). This prediction has now been borne out in laboratory studies for the uptake of ammonium and nitrate (Eppley *et al.*, 1969) and for vitamin B_{12} (Carlucci, unpublished, cited in Eppley, 1972). Furthermore, buoyancy is related to cell size (Smayda, 1970), as is grazing pressure (Mullin, 1963; Smayda, 1973a). Because of these differences it would be desirable to fractionate the natural phytoplankton population into different size-classes as a way of beginning to understand the relative importance of the different parts of the community,

and to describe the behaviour of individual species for a given particular set of environmental conditions.

Previous size-fractionation studies have been concerned with sampling and describing the community; the problem of species succession was not a primary aim (Holmes, 1958; Yentsch and Ryther, 1959; Gilmartin, 1964; Anderson, 1965; Saijo and Takasue, 1965; Malone, 1971a, b). Holmes, Anderson, Saijo and Takasue and Malone (1971a) found that in a variety of oceanic environments nannoplankton (that fraction not retained by the fine-mesh net used, generally 20 to 60 µm) are often responsible for 80 to 99% of the observed production. In neritic waters in the Eastern Tropical Pacific and the Caribbean Sea Malone (1971a) found that netplankters (> 25 µm) were more important, contributing approximately 50% of the total production measured at these stations. Seasonal studies in neritic waters in Vineyard Sound (Yentsch and Ryther, 1959) and in the California Current off Monterey Bay (Malone, 1971b) showed the nannoplankton population to be the most important and relatively stable, while the netplankton showed marked seasonal trends, increasing when conditions became favourable for diatom growth during the winter-spring bloom or during periods of upwelling. At high latitudes, where the phytoplankton is made up mostly of chain-forming diatoms, the netplankton is also relatively more important (Digby, 1953). However, the relative importance of nannoplankton and netplankton in northern temperate and boreal coastal waters is not well documented, particularly with respect to any seasonal changes that may occur.

In this study the phytoplankton population in Narragansett Bay was fractionated into four size-classes and the cell numbers and species composition, chlorophyll *a*, ATP levels and rates of carbon assimilation were determined for each size class. This study is part of a program to more clearly define the successional changes in the composition of the different size classes, the rates at which these different fractions turn over, and to assess the role of individual species.

Materials and Methods

Around 09.00 hrs every second week from November 27, 1972 to October 15, 1973, a sample was collected from the bottom (9 m), mid-depth, and at the surface in 10-l Niskin bottles, at Station 2 (see Pratt, 1959) in lower Narragansett Bay. Equal parts (6.25 l) from the three depths were combined to obtain a mixed sample. In the laboratory this sample was fractionated by filtering it successively through filter funnels with Nitex cloth of 100, 60 and 20-µm mesh size. Each filter-funnel consisted of a 13-cm length of 6.5 cm inner-diameter plexiglass tubing glued to a plexiglass base, to which Nitex cloth was permanently attached (Fig. 1). A base of flat plexiglass plate with a rubber tube leading from the centre of it to a collecting vessel was clamped to the filter-funnel; a rubber O-ring separated the two plates to make it water-tight. A clamp on the rubber outlet tube controlled the flow-rate through the filter. The whole rig was supported by a ring clamp placed under the filter base.

In carrying out the fractionation, water was passed through the 100-µm filter, taking care not to drain the filter completely dry. When about 50 ml of water remained above the filter the drain-tube was clamped off, filtered seawater from the same day's sample was added to the concentrated sample, and following gentle swirling to dislodge cells resting on the filter, the contents were poured into a measuring cylinder and made up to the desired volume with filtered seawater. The few milliliters of water remaining under the filter were drained into the vessel containing the filtrate. This procedure was repeated with the 60-µm and the 20-µm filters so that > 100, 60-100 and 20 to 60-µm fractions of known concentration and an unconcentrated < 20-µm fraction were obtained. Generally 2 l of sample were filtered and the concentrate made up to 500 ml, giving a concentration factor of 4X. Throughout the procedure flasks containing the samples were kept in a water bath to prevent warming.

Carbon-assimilation rate, chlorophyll concentration, ATP level and cell numbers were determined for each size fraction. Rates of carbon assimilation were estimated by the C-14 method (Steemann Nielsen, 1952). Samples (50 ml) were inoculated with about 1 µCi of bicarbonate C-14. These were placed in a tank containing running seawater located on the School of Oceanography dock, and incubated under ambient light from about noon to sundown on the day of sample collection. Following incubation, the samples were filtered on membrane filters, dried and counted on a Nuclear-Chicago Model 4338 planchet counting system. Chlorophyll *a* and phaeopigments were determined by fluorometry (Yentsch and Menzel, 1963) using a red-sensitive phototube (R-176) and the equations of

Lorenzen (1966). ATP was determined by the method of Holm-Hansen and Booth (1966) as modified by Cheer *et al.* (1974). Cell numbers were determined by counting a 1.0-ml sample in a Sedgwick-Rafter chamber. If samples were not counted immediately, Lugol's iodine solution was added as a preservative.

Results

Species Composition

Cell numbers for the different size fractions are shown in Fig. 2; the composition and abundance are given in Table 1. Because many species of diatoms form long chains or have long setae, or both, the cells retained by filters do not necessarily have dimensions greater than the filter mesh-size. This effect was particularly noticeable during the winter-spring bloom when chain-forming diatoms predominated, and when small cells such as *Skeletonema costatum*, *Detonula confervacea* or *Chaetoceros compressus* were found in the largest size fraction. However, the population was fractionated

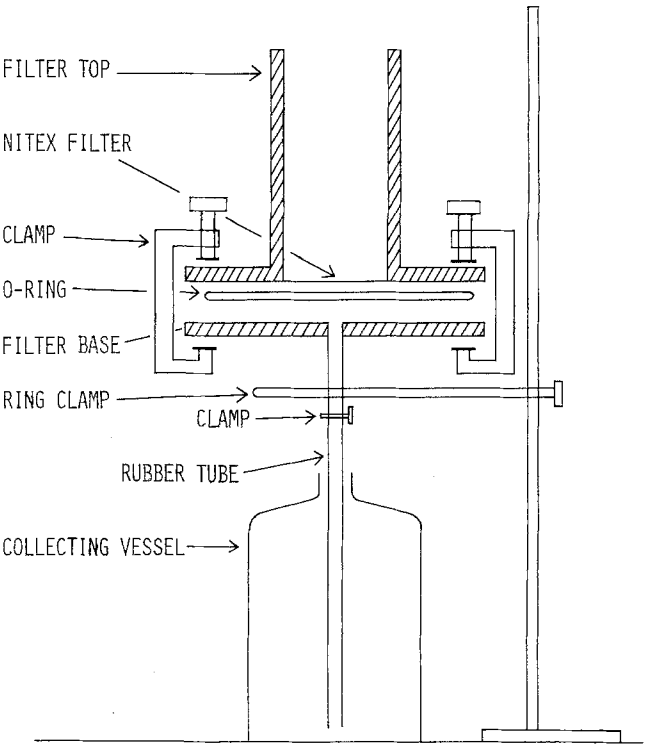

Fig. 1. Filter apparatus used to size fractionate natural phytoplankton population

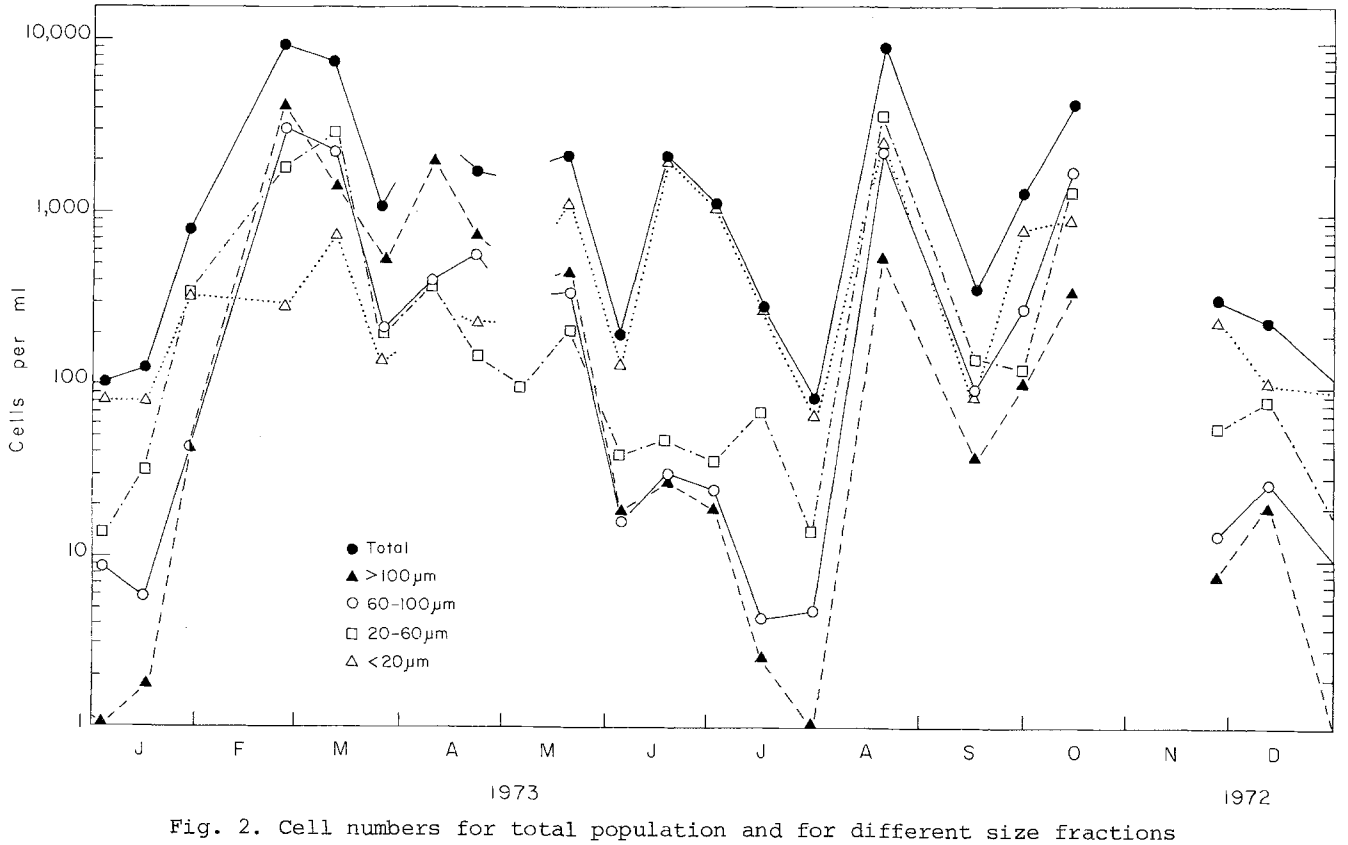

Fig. 2. Cell numbers for total population and for different size fractions

Table 1. Cell counts (cells/ml) for different size fractions (A: >100 µm; B: 60 to 100 µm; C: 20 to 60 µm; D: <20 µm); N.C.: counts not made

Species	1972								1973											
	27 November				14 December				2 January				15 January				29 January			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Attheya decora			2.7				15.9													
Actinoptychus undulatus							0.1			0.5										
Asterionella japonica			3.7		1.5		0.6			3.2							8.2			
Cerataulina pelagica						0.1														
Chaetoceros affinis	3.6																			
C. decipiens																				
C. densus	0.3	0.4																		
C. diadema					2.4	0.7				1.2										
C. didymus					0.5															
C. laciniosus					0.7	0.8							1.0							
C. subsecundus	0.6																23.8			
Chaetoceros sp.		1.1					4.2								1.5			3.7	58.0	
Corethron hystrix		0.1	0.2				0.5				0.1				0.3					
Cyclotella sp.			0.2										0.3			30.0				
Detonula confervacea			2.5															16.0	19.3	
Ditylum brightwellii		0.1																		
Leptocylindrus minimus				4.0		0.5									0.8					
Nitzschia closterium											0.2	0.2			0.3				2.4	
N. reversa																		0.2	1.2	
N. seriata		0.7																		
Paralia sulcata							2.6				1.0				0.8				6.6	
Rhizosolenia setigera										0.1	0.1		0.5					1.2		
Skeletonema costatum		8.5	24.5	94.0	14.0	24.4	51.1	52.0		1.9	6.6	8.0		4.3	19.3	38.0	9.0	18.0	222.0	168.0
Thalassiosira decipiens		0.1	5.7			6.5	4.6			0.2	3.7			1.0	2.5				1.8	
T. nordenskioeldii																		1.7		
Thalassiosira sp.	3.4	3.1	6.7	140.0	1.0	0.7	2.5	56.0	0.1	0.4	0.5	2.0			3.8	10.0	2.0	1.0	35.4	99.0
Thalassionema nitzschioides			2.0												1.0					
Thalassiothrix frauenfeldii											0.4				0.4					
Pennate							0.1	4.0						0.5	0.8	4.0				
Peridinium sp.	0.1	0.1	0.7	2.0	0.2	0.1	0.1	2.0			0.1					4.0				
Microflagellates				N.C.				N.C.				56.0				18.0				71.0
Total cells	8.1	14.2	59.2	240.0	20.4	27.9	82.4	114.0	0.1	8.6	13.4	80.0	1.8	5.8	31.9	80.0	44.0	42.0	352.0	337.0

Species	1973																			
	26 February				12 March				26 March				9 April				23 April			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Asterionella japonica					146.0	139.0			23.5				73.0	16.3			128.0	16.3		
Chaetoceros compressus									38.0				489.0	105.0	11.0		186.0	369.0	27.6	
C. decipiens									69.0	5.0			565.0	16.7			15.4	2.7		
C. diadema	54.3				10.0	9.0	9.0													
C. didymus																				
Chaetoceros sp.	9.0		8.7		9.0	40.0	99.0	23.2	3.6		1.4	0.5		14.5						
Detonula confervacea	2780.0	1939.0	700.0	10.0	451.0	1037.0	901.0	89.9		21.0	32.0	52.0			119.0					
Leptocylindrus danicus															22.0		263.0	90.6	82.9	61.0
L. minimus																			9.5	43.5
Nitzschia closterium								2.9				12.0			3.6		1.8			
N. seriata										1.4			50.7	10.8	3.6		12.7	11.0		
Pennate sp.			14.5								0.72	3.0	25.4	5.4	18.0					
Rhizosolenia alata																	0.9			
R. delicatula						19.0							87.0	20.0						
R. fragilissima							9.0		16.3	5.0	5.9			16.3				16.9	3.1	
R. imbricata var. *shrubsolei*																				
R. setigera	9.0				2.0	1.0			1.8								5.4	2.7		
Skeletonema costatum	692.0	931.0	719.0	103.0	471.0	892.0	1733.0	565.0		5.8	21.7	61.0	14.5	5.4	65.0		1.8	1.8	1.8	
Thalassiosira decipiens			29.0																	
T. nordenskioeldii	558.0	46.4	5.8		339.0	125.0	51.0		391.0	177.6	128.0	8.0	714.0	186.7	76.0		10.8	26.3	19.4	
T. rotula		11.6																		
Thalassiosira sp.	87.0	52.2	282.0	162.0		9.0	23.0	23.0					25.0							
Thalassionema nitzschioides	3.6																			
Peridinum trochoideum								2.0												
Peridinum sp.			4.3								1.4									5.8
Microflagellates				N.C.				N.C.				N.C.				N.C.				110.0
Choanoflagellate	90.6	116.0	62.3	7.0																
Euglenid				1.0				55.1												
Dinobryon sp.						1.0		14.5												
Phaeocystis pouchetii					2.0															
Total cells	4193	3099	1799	283	1430	2272	2837	770	544	216	194	136.5	2046	404	367	N.C.	764	578	144	228.8

Continued on p. 276

Table 1. (Continued)

Species	1973																			
	7 May				21 May				4 June				18 June				2 July			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Asterionella japonica			3.0		292.0	229.0	25.4			0.5	1.5						2.0			
Chaetoceros compressus					72.5	14.5			15.2	10.0	1.7			3.0						
C. diadema													0.7							
C. didymus									2.0											
Chaetoceros sp.			2.9										0.2	0.2			0.2			
Dactyliosolen sp.													0.2							
Ditylum brightwellii					1.2					0.2	1.0									
Leptocylindrus minimus			2.33		66.4	99.1	165.8	710.0		2.7	6.0	46.0	1.0	3.7	3.9	28.0				
Rhizosolenia alata									0.5											
R. delicatula							2.7						2.0	1.2	3.5					
R. fragilissima			81.1	65.3																14.0
Skeletonema costatum							16.3	70.0	1.0	1.0	8.0	16.0			3.1		1.5	2.9		
Thalassiosira rotula											4.5		0.7	1.2	17.1				1.3	28.0
Thalassiosira sp.			1.7																	
Cyclotella sp.																	0.7		4.6	70.0
Nitzschia closterium			2.3		2.4	2.4	1.8	14.5		0.5		6.0		0.2	0.4		0.5		1.3	14.0
N. seriata					15.7	4.8			1.5	0.2			10.2	2.7	0.8					
Thalassionema nitzschioides																			1.3	
Pennate			2.9	9.3						0.2	0.2									
Dinophysis sp.															3.5		0.2		0.6	7.0
Gymnodinium sp.													1.2	3.0	3.5	56.0				63.0
Prorocentrum redfieldii													4.5	2.2	3.1	126.0	0.2	0.6	0.6	49.0
Prorocentrum sp.																				
Peridinium sp.									0.5	0.5	2.2	2.0	0.2	1.6	1.6	28.0				7.0
Dinoflagellate				23.3																
Microflagellates				N.C.				362.0			2.7	40.0	5.5	2.7		280.0				35.0
Olisthodiscus luteus													3.7	8.7	8.5	1582.0	13.5	21.0	27.4	770.0
Total cells	N.C.	N.C.	95.5	97.8	450	349	213	1156	19.7	16.0	38.7	130.0	28.5	31.7	48.8	2100.0	19.2	25.1	37.2	1057.0

Species	1973																							
	16 July				30 July				20 August				17 September				1 October				15 October			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Asterionella japonica				3.2					78.7	471.0	267.0		3.5	1.4	5.8		22.1	156.7			217.0	532.0	42.0	
Chaetoceros compressus										15.7														
C. curvisetus																	20.4	21.9	5.2					
C. decipiens									8.7	19.2	10.5						8.2				21.0	21.0		
C. didymus									6.1	43.2	52.5													
Chaetoceros sp.	0.5	0.2					0.5		3.5		2.3		15.8	12.6	9.3		4.2	7.9	10.5		45.5	14.0	5.25	28.0
Corethron hystrix							0.7							0.7	1.2									
Coscinodiscus sp.						0.2	1.7		0.4															
Cyclotella sp.			1.0	5.6			5.0	5.0																
Dactyliosolen mediterraneus							0.2																	
Ditylum brightwellii						0.5			1.3	3.5	2.3		0.8	4.9	2.3		0.6	3.5	4.3					
Eucampia zoodiacus														1.4				6.1	3.2			14.0	42.0	
Leptocylindrus danicus															5.8	11.6								
L. minimus														1.4	7.0				7.9				12.2	
Paralia sulcata							1.0																	
Rhizosolenia fragilissima	2.2	3.5	2.2	11.2		4.0	5.0	12.0					17.6	7.7	4.6	7.0								
R. hebetata f. *hemialis*					0.2																			
Skeletonema costatum									472.0	1967.0	1864.0	3108.0	3.5	49.0	54.8		5.8	7.8	14.0	14.0		1113.0	1249.0	928.0
Thalassiosira rotula																						7.0	9.3	
Thalassiosira sp.											2.3	70.0			14.0	4.6	36.1	79.6	39.5	779.0	45.5	14.0	12.2	23.0
Nitzschia closterium							0.5	2.0	0.4	1.7			3.5	2.1	19.8	14.0	1.2	0.9	0.8				1.7	
N. seriata									4.8	3.5			8.7	10.5	2.4		3.5							
Thalassionema nitzschioides													1.7	4.9	16.3	46.6	6.4		41.1	23.3				18.6
Pennate							0.7	5.0							1.2	4.6			0.8					
Ceratium furca						0.5																		
Dinophysis sp.																		0.8						
Gymnodinium sp.				14.0				1.0																
Prorocentrum redfieldii																								
Prorocentrum sp.																		0.8						
Peridinium sp.											1.2			0.7										
Microflagellates		0.7	3.5	226.0			3.0	41.0				546.0												
Olisthodiscus luteus			0.5	22.4																				
Total cells	2.7	4.5	7.2	283.2	0.2	5.0	14.5	66.0	570.0	2534.0	2172.0	3724.0	38.4	97.3	145.8	88.4	115.4	292.0	128.2	816.0	329.0	1715.0	1364.0	928.0

to some extent, even though not strictly according to size. For example, during the winter-spring bloom when long chains of *Thalassiosira nordenskiöldii, S. costatum* and *D. confervacea* were numerous, *T. nordenskiöldii* was retained principally in the > 100-µm fraction, while the other two species were found in all three fractions > 20 µm, but were relatively more important in the 60 to 100-µm and 20 to 60-µm fractions.

During the minimum prior to the winter-spring bloom in February, small cells < 20 µm dominated the plankton, particularly *Skeletonema costatum,* a small solitary *Thalassiosira* sp., and microflagellates. Several diatom species were found in the larger fractions during this period, but were not important numerically. By February 26 the winter-spring bloom reached its initial peak. *Detonula confervacea, S. costatum, T. nordenskiöldii,* and the solitary *Thalassiosira* sp. dominated (Table 1). At this stage most of the cells were found in the two largest fractions (7292 cells out of a total of 9374 cells/ml). These species remained dominant in early March but, by March 26, *S. costatum* and *D. confervacea* had disappeared almost completely. *T. nordenskiöldii* remained the sole dominant in the > 100 and 60 to 100-µm fractions. At this time the total population had decreased from 12,370 cells/ml and 7310 cells/ml on the previous two sampling dates to 1090 cells/ml.

Following this decline, two successive peaks in abundance occurred: on April 9 and on May 7. In each of these the group of dominant species changed; *Chaetoceros compressus, C. decipiens* and *Thalassiosira nordenskiöldii* dominated on April 9. *T. nordenskiöldii* then dropped out, and the *Chaetoceros* spp. were joined by *Asterionella japonica, Leptocylindrus danicus* and *L. minimus*. During the entire winter-spring bloom the > 100-µm fraction was the most important numerically.

Large numbers of *Olisthodiscus luteus* were present during June, when the nannoplankton (< 20 µm) fraction became dominant as cell numbers. Flagellates completely dominated thereafter throughout the summer, and few diatoms were present until August 20.

A late-summer and early-fall bloom of *Skeletonema costatum* occurred, most of the cells were found in the < 20-µm and 20 to 60-µm fractions. Its initial peak on August 21 was followed by a period when several diatom species dominated the sparse population.

Standing Crop Measurements

Marked seasonal changes in the chlorophyll *a* content of all size fractions occurred (Fig. 3, Table 2). On the average, the < 20-µm fraction was the most important; it comprised 46.6% of the annual biomass as chlorophyll *a*.

The nannoplankton (< 20 µm) fraction was most important during the mid-winter minimum (December-January) and during the summer (4 June-20 August). Over 75% of the chlorophyll *a* was then in this size class. Almost half (44%) of the total nannoplankton standing crop (as chlorophyll *a*) was found during the summer period.

During the spring and fall diatom-blooms, netplankters (> 20 µm) predominated, especially from 26 February - 7 May, when 77% of the total chlorophyll *a* for this period was contained in this size fraction.

Lowest chlorophyll *a* levels were recorded during the mid-winter minimum (< 1.3 mg chlorophyll *a*/m^3). Levels increased thereafter during the winter-spring bloom, characterized by considerable fluctuations and three successive peaks (Fig. 3). Over 50% of the total chlorophyll *a* at the time of these occurred in the > 100-µm fraction because of the predominance of long-chained diatoms (Fig. 2). During the initial peak (February 26), cell numbers and chlorophyll *a* were at a maximum for the bloom period (12,370 cells/ml and 9.78 mg chlorophyll *a*/m^3).

During the summer, chlorophyll *a* levels were generally quite high; a July (16) peak of 11.85 mg chlorophyll *a*/m^3 occurred. Cell numbers, however, were frequently low and dominated by flagellates < 20 µm. For example, on June 18, total cell numbers reached their summer maximum of 2209 cells/ml, of which 2000 cells/ml were in the < 20-µm fraction (Fig. 2; Tables 1, 2).

Diatoms dominated the fall peaks observed on August 20 and October 15 (Figs. 2, 3); the > 20-µm fractions then became relatively more important. Although cell numbers were then much higher (9000 and 4300 cells/ml, respectively) than in the summer, the chlorophyll *a* levels (4.31 and 8.04 mg chlorophyll *a*/m^3) were lower.

Throughout the year, the cell counts for the < 20-µm fraction were much lower than expected from the chlorophyll *a* levels, which suggests that the method used to count cells did not reliably estimate those < 20 µm. This discrepancy was most important during the summer when flagellates dominated the population. For example, on July 16 the chlorophyll *a* level in the < 20-µm fraction reached its annual maximum (10.96 mg chlorophyll *a*/m^3), but only 283 cells/ml were enumerated.

The ATP content of each size fraction was multiplied by a factor of 250 to obtain phytoplankton carbon content (Holm-Hansen, 1969, 1970); this value has been used by most other workers (e.g. Sutcliffe *et al.*, 1970; Eppley *et al.*, 1973). The carbon content of the different size fractions (Fig. 4, Table 2) generally followed the chlorophyll *a* trends, although occasionally values were higher than expected from the chlorophyll *a* levels. High C:chlorophyll *a* ratios then resulted (Table 2), especially on June 18 (125) and October 1 (149).

Production

Fig. 5 and Table 2 give the rates of carbon assimilation for each fraction, and as a percent of the assimilation of the total community. For the chlorophyll *a* content, the < 20-µm fraction was most important; it contributed 50.8% of the total annual production and 88% of that measured during the summer period (4 June - 20 August). Production in the netplankton fractions was greatest during the winter-spring and fall diatom-blooms.

Production was high throughout the year (> 5 mg C/m^3/h), except during the phytoplankton minimum prior to the winter-spring bloom. The maximum assimilation rate of 82.4 mg C/m^3/h and minimum of 1.34 mg C/m^3/h were measured on July 16 and January 15, respectively. The mean assimilation rate over the annual cycle was 18.4 mg C/m^3/h.

Specific Growth Rates of the Phytoplankton

Phytoplankton growth rates as doublings of carbon per day were determined, based on the rate of carbon assimilation per unit of living carbon from:

$$\mu = \left(\frac{1}{t}\right) \log_2 \left(\frac{C_1 + \Delta C}{C_1}\right),$$

in which ΔC is the daily increase in carbon due to photosynthesis, C_1 is the carbon content of the phytoplankton, and μ the specific growth rate as doublings of carbon per day (t = 1). The values for ΔC were obtained by multiplying the hourly assimilation rates by the number of daylight hours for that day. Values for C_1 were determined in two ways: Prior to the ATP measurements it was estimated from (chlorophyll *a*) (60), in which 60 is the assumed C: chlorophyll *a* ratio. Little information exists on the C: chlorophyll *a* ratios of the diatoms present in the winter-spring bloom in Narragansett Bay. A ratio of 67 was obtained for a natural, almost pure population of *Skeletonema costatum* growing at 12°C *in situ* within the 20 to 60-µm fraction which contained little detrital material. A ratio of 57 was obtained for *Thalassiosira nordenskiöldii* growing in dialysis sacs at 9°C. These observations suggest the ratio of 60 used. However, since a lower C:chlorophyll *a* ratio may characterize the beginning of the winter-spring bloom because of the lower temperatures and light intensities (Eppley, 1972), this value probably then overestimates the phytoplankton carbon and gives lower carbon doubling-rates. Accordingly, phytoplankton carbon doubling-rates were calculated only for the whole population during the winter-spring bloom (Fig. 6; Table 2).

C_1 was also estimated from ATP. These estimates of phytoplankton carbon are probably much more reliable then those based on the C:chlorophyll *a* ratio,

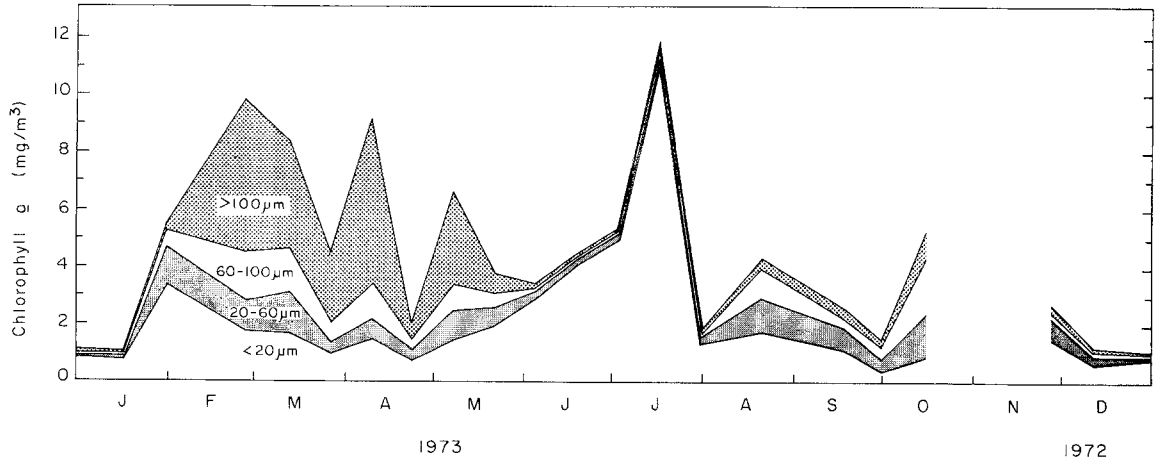

Fig. 3. Cumulative graph of chlorophyll *a* content of different size fractions

Table 2. Chlorophyll *a* (Chl *a*), phaeopigment (Phaeo) and ATP concentrations; carbon fixation and carbon doubling (*K*) rates and assimilation number (Assim. no.) for different size fractions during annual cycle. Prod.:production

Size fraction (µm)	Temperature (°C)	Chl *a* (mg/m³)	Phaeo (mg/m³)	Phaeo / Chl *a*	ATP (mg/m³)	Cell C (mg/m³)	C / Chl *a*	Prod. (mgC/m³) h	% total Prod.	Daily Prod. (mgC/m³) day	Assim. no.	*K*
27.XI.1972	7.0											
>100		0.20	0.10	0.50				0.25	4.1		1.25	
60-100		0.21	0.06	0.28				0.38	6.2		1.81	
20-60		0.81	0.18	0.22				1.28	20.8		1.58	
<20		1.52	0.90	0.59				4.23	68.9		2.78	
Total		2.74	1.24	0.45				6.14		65.2		
11.XII.1972	6.0											
>100		0.11	0.03	0.27				0.15	4.7		1.36	
60-100		0.17	0.03	0.18				0.19	5.9		1.12	
20-60		0.27	0.03	0.11				0.48	14.9		1.78	
<20		0.69	0.43	0.62				2.39	74.4		3.46	
Total		1.24	0.52	0.42				3.21		33.5		
2.I.1973	4.5											
>100		0.014	0.004	0.28				0.037			2.64	
60-100		0.034	0.009	0.26				0.051			1.5	
20-60		0.099	0.019	0.19								
<20		0.87	0.19	0.22								
Total		1.02	0.22	0.21								
16.I.1973	0.5											
>100		0.066	0.018	0.27				0.08	6.0		1.29	
60-100		0.042	0.009	0.21				0.04	3.0		0.97	
20-60		0.11	0.024	0.22				0.104	7.8		0.95	
<20		0.79	0.27	0.34				1.12	83.6		1.43	
Total		1.01	0.32	0.32				1.34		14.3		
29.I.1973	4.2											
>100		0.50	0.005	0.00				0.99	12.4		1.97	
60-100		0.56	0.03	0.05				0.88	10.0		1.42	
20-60		1.34	0.08	0.06				2.27	28.5		1.69	
<20		3.38	0.28	0.21				3.89	48.9		1.16	
Total		5.78	0.40	0.07				8.03		89.1		
26.II.1973	1.8											
>100		5.28	0.00	0.00				17.1	49.8		3.24	
60-100		1.71	0.00	0.00				6.91	20.8		4.04	
20-60		1.07	0.00	0.00				5.07	14.7		4.74	
<20		1.72	0.34	0.19				5.27	15.3		3.06	
Total		9.78	0.34	0.03		586[a]	60	34.3		343		0.65[a]
12.III.1973	5.5											
>100		3.49	0.05	0.01				7.46	34.1		2.13	
60-100		1.54	0.30	0.19				6.28	28.6		4.08	
20-60		1.42	0.42	0.29				5.64	25.7		3.98	
<20		1.70	1.07	0.63				2.52	11.5		1.48	
Total		8.35	1.74	0.20		501[a]	60	21.9		720		0.52[a]
26.III.1973	5.0											
>100		2.42	8.10	0.04				4.69	55.1		1.94	
60-100		0.70	0.02	0.03				1.62	19.0		2.32	
20-60		0.37	0.09	0.24				0.67	7.9		1.83	
<20		0.99	0.55	0.55				1.52	17.9		1.53	
Total		4.46	0.77	0.19		267[a]	60	8.50		352		0.39[a]
9.IV.1973	6.0											
>100		5.65	0.26	0.04				15.0	56.6		2.66	
60-100		1.30	0.04	0.03				5.21	19.6		4.01	
20-60		0.69	0.16	0.23				2.26	8.5		3.28	
<20		1.49	0.54	0.36				4.04	16.6		2.71	
Total		9.13	0.80	0.09		547[a]	60	26.5		812		0.57[a]
23.IV.1973	8.5											
>100		0.50	0.10	0.20	0.20	50	100	1.26	31.3	17.6	2.51	0.43
60-100		0.35	0.04	0.11	0.10	25	71.4	0.92	22.8	12.9	2.61	0.59
20-60		0.40	0.02	0.05	0.10	25	62.5	0.62	15.4	8.7	1.55	0.43
<20		0.76	0.49	0.64	0.45	112	148	1.22	30.3	17.1	1.60	0.20
Total		2.01	0.65	0.32	0.85	212	105	4.02		56.2		0.34
7.V.1973	11.4											
>100		3.23	0.29	0.09	0.86	215	66.5	16.1	60.8	241.0	4.97	1.08
60-100		0.91	0.16	0.17	0.24	60	65.9	4.37	16.5	65.5	4.80	1.06
20-60		1.05	0.15	0.14	0.24	60	57.1	2.64	9.9	39.6	2.52	0.73
<20		1.42	0.69	0.50	0.66	165	113	3.57	13.5	53.5	2.51	0.41
Total		6.61	1.28	0.19	2.00	500	75.6	26.7		400.0		0.85

Size fraction (µm)	Tem-pera-ture (°C)	Chl *a* (mg/m³)	Phaeo (mg/m³)	Phaeo / Chl *a*	ATP (mg/m³)	Cell C (mg/m³)	C / Chl *a*	Prod. (mgC/m³)/h	% total Prod.	Daily Prod. (mgC/m³)/day	Assim. no.	*K*
21.V.1973	13.0											
>100		0.75	0.07	0.01	0.29	72.5	96.6	2.54	25.2	38.1	3.38	0.61
60-100		0.47	0.09	0.19	0.14	35	74.5	1.07	10.6	16.0	2.28	0.54
20-60		0.66	0.14	0.21	0.23	57.5	87	1.73	17.1	25.9	2.62	0.54
<20		1.94	0.97	0.29	0.86	215	112	4.76	47.1	71.4	2.45	0.41
Total		3.91	1.15	0.29	1.52	380	97.2	10.1		151.0		0.48
4.VI.1973	14.0											
>100		0.16	0.07	0.43				0.46	3.4	6.9	2.87	
60-100		0.12	0.06	0.50				0.36	2.6	5.6	3.00	
20-60		0.25	0.11	0.43				0.88	6.5	13.2	3.52	
<20		2.91	1.02	0.35				11.9	87.5	178.0	4.10	
Total		3.44	1.23	0.36				13.6		204.0		
18.VI.1973	16.5											
>100		0.13	0.05	0.38	0.16	40	307	0.44	2.1	6.9	3.37	0.23
60-100		0.11	0.04	0.37	0.09	22.5	204	0.42	2.0	6.6	3.79	0.37
20-60		0.18	0.06	0.33	0.14	35	194	0.95	4.4	15.0	5.29	0.51
<20		4.07	0.79	0.19	1.86	465	114	19.5	91.5	308.0	4.80	0.73
Total		4.49	0.84	0.19	2.25	562	125	21.3		336.0		0.68
2.VII.1973	19.0											
>100		0.13	0.04	0.31	0.14	35	269	0.17	1.9	2.5	1.31	0.10
60-100		0.12	0.04	0.33	0.05	12.5	104	0.22	2.5	3.3	1.83	0.34
20-60		0.18	0.09	0.50	0.09	22.5	125	0.40	4.6	6.6	2.22	0.37
<20		4.92	0.86	0.17	1.03	257	52	7.96	91.0	119.0	1.61	0.56
Total		5.35	1.03	0.21	1.31	327	61.1	8.75		131.0		0.48
16.VII.1973	21.0											
>100		0.28	0.15	0.55	0.19	47.5	169	2.88	3.6	42.5	10.3	0.92
60-100		0.29	0.15	0.53	0.07	17.5	60	1.69	2.1	24.9	5.8	1.27
20-60		0.32	0.27	0.59	0.06	15	46.8	2.66	3.3	39.2	8.3	1.85
<20		10.96	2.94	0.27	1.52	380	34.6	73.1	91.0	1078	6.7	1.94
Total		11.85	3.51	0.31	1.84	460	38.8	80.3		1184		1.84
30.VII.1973	19.5											
>100		0.08	0.10	1.25	0.16	40	333	0.79	5.9	11.3	6.58	0.36
60-100		0.11	0.12	1.10	0.03	7.5	68	0.58	4.4	8.3	5.27	1.07
20-60		0.14	0.14	1.00	0.04	10	71	0.94	7.1	13.5	6.71	1.23
<20		1.45	1.19	0.83	0.30	75	52	11.0	82.6	158.0	7.58	1.63
Total		1.78	1.54		0.54	135	758	13.3		190.0		1.27
21.VIII.1973	22.0											
>100		0.34	0.23	0.66	0.075	18.7	55	0.36	5.1	5.0	1.08	0.39
60-100		1.05	0.51	0.47	0.23	57.5	55	1.20	17.0	16.8	1.14	0.37
20-60		1.19	0.85	0.71	0.37	92.5	78	1.90	26.9	26.6	1.59	0.36
<20		1.77	1.43	0.83	0.56	140.0	79	3.60	51.0	50.4	2.03	0.44
Total		4.35	3.02	0.69	1.24	409.0	94	7.06		99.0		0.40
17.IX.1973	22.0											
>100		0.30	0.10	0.33	0.18	45.0	150	2.75	11.9	36.6	9.16	0.86
60-100		0.31	0.12	0.38	0.14	35.0	113	2.45	10.7	32.6	7.90	0.95
20-60		0.81	0.26	0.32	0.27	77.5	96	7.51	32.7	100.0	9.27	1.19
<20		1.12	0.31	0.28	0.39	97.5	87	10.25	44.6	136.0	9.15	1.26
Total		2.54	0.79	0.31	0.98	245.0	96	22.90		304.0		1.16
1.X.1973	17.0											
>100		0.22	0.03	0.14	0.097	24	111	1.53	10.9	17.2	6.95	0.77
60-100		0.44	0.09	0.22	0.21	52	119	3.62	25.7	40.7	8.23	0.83
20-60		0.44	0.29	0.67	0.21	52	119	3.55	25.2	39.9	8.07	0.82
<20		0.39	0.83	2.10	0.37	92	237	5.48	38.9	61.6	14.05	0.73
Total		1.49	1.22	0.81	0.89	222	149	14.20		159.7		0.85
15.X.1973	15.0											
>100		0.82	0.04	0.05	0.17	42	52	4.37	12.4	48.1	5.33	1.09
60-100		2.00	0.37	0.18	0.26	65	32	12.2	34.5	134.2	6.00	1.61
20-60		1.53	0.42	0.33	0.19	47	31	12.1	34.5	133.0	7.88	1.93
<20		0.96	0.95	0.98	0.26	65	68	6.67	18.9	73.4	6.95	1.08
Total		5.31	1.78	0.34	0.88	220	41	35.3		388.0		1.47

[a] Values calculated from C:chlorophyll *a* ratio of 60. Rest of numbers for cellular C (Cell C) calculated from ATP.

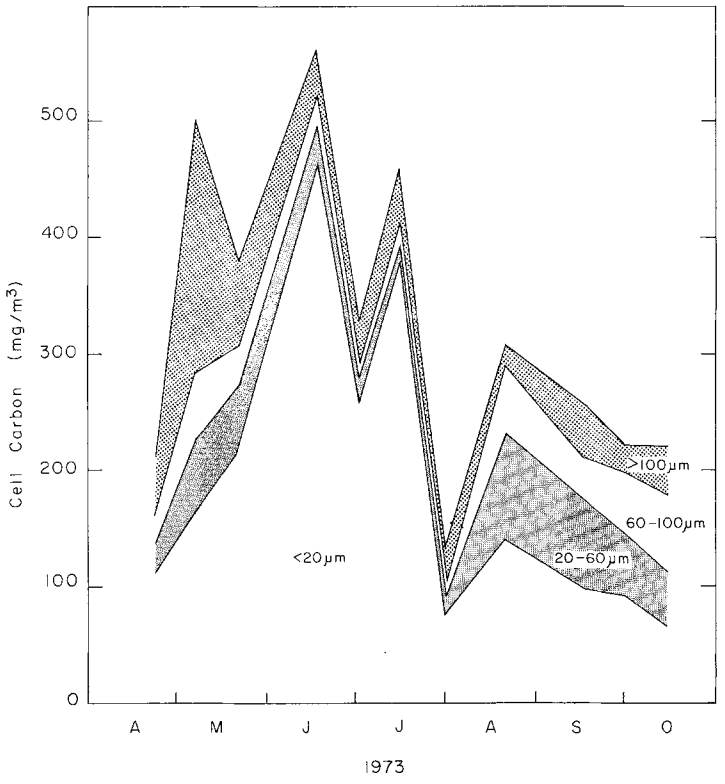

Fig. 4. Cumulative graph of carbon content of different size fractions, estimated from ATP concentration

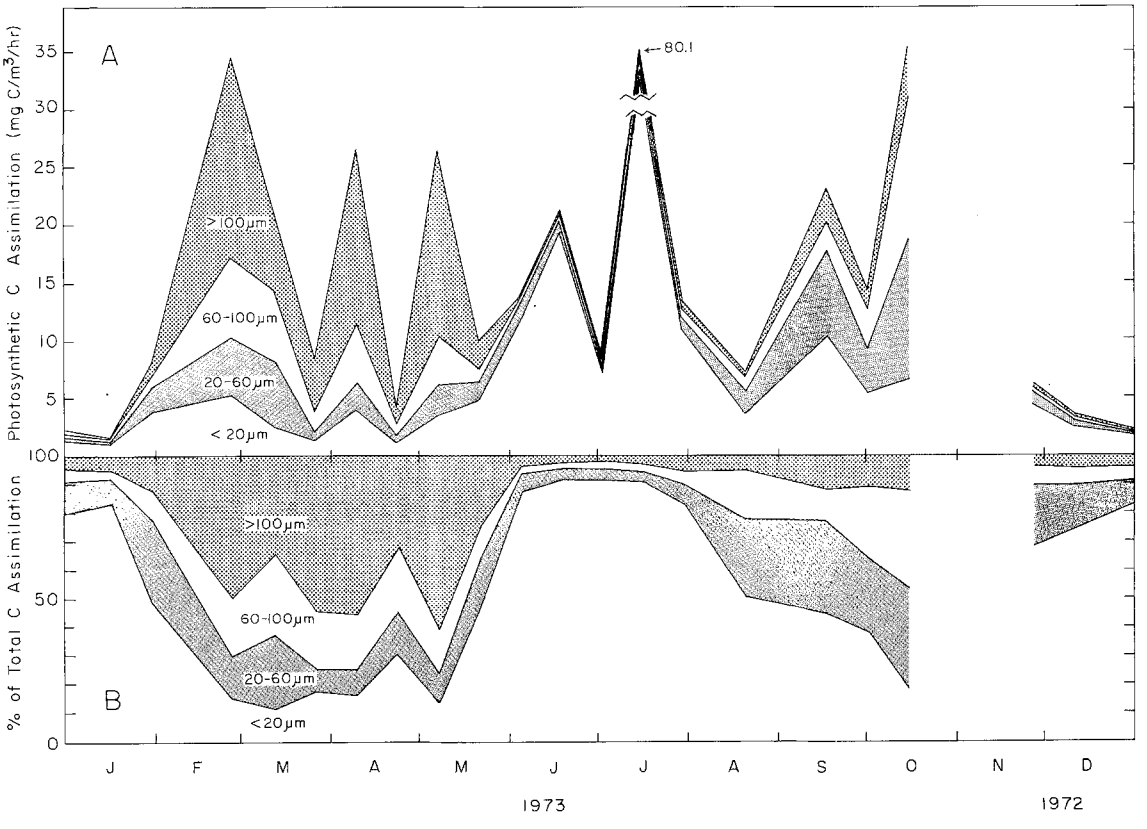

Fig. 5. (A) Cumulative graph of photosynthetic carbon assimilation by different size fractions of phytoplankton; (B) photosynthetic carbon assimilation by different size fractions as percentage of total population response

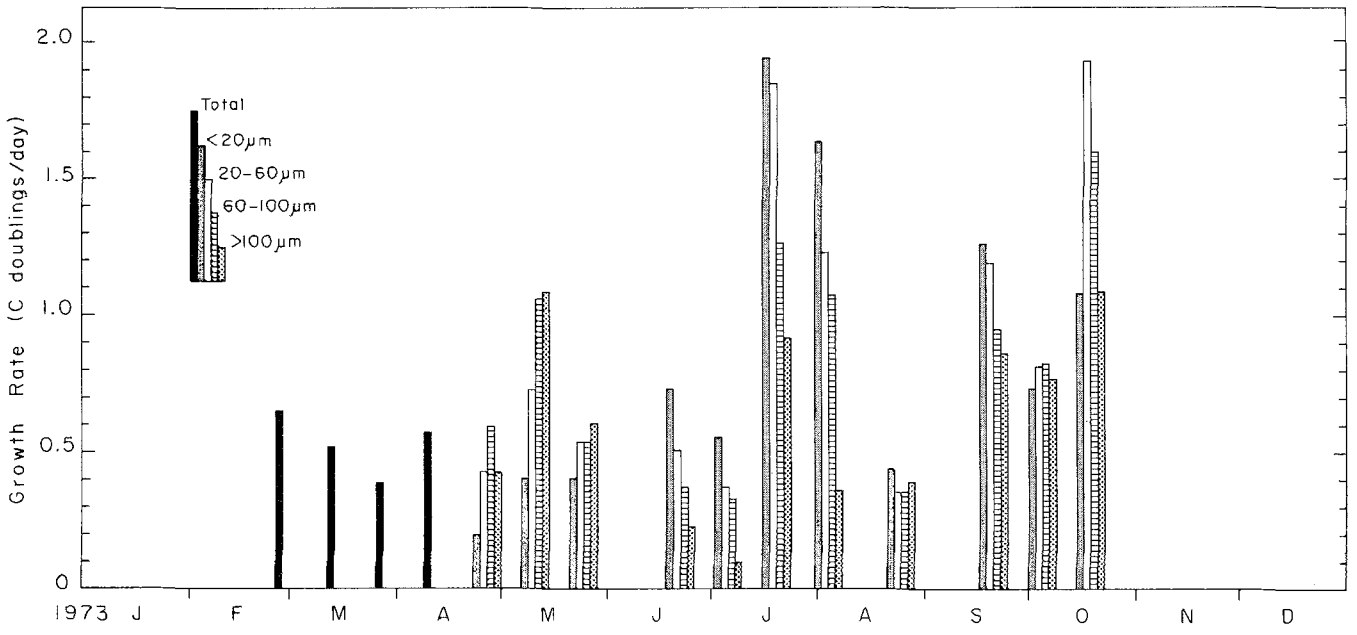

Fig. 6. Growth rates as carbon doublings per day for different size fractions and for total phytoplankton population (see text for further details)

since ATP appears to show a much more constant relationship to cell carbon (Holm-Hansen, 1970). Carbon doubling-rates based on these estimates of C_1 were calculated for each size fraction sampled from the end of April to October (Fig. 6; Table 2).

During the winter-spring bloom, doubling rates were not high; the maximum was slightly > 1 per day on May 7. During the bloom's initial peak, the mean rate was only 0.65. Diatoms in the size fractions > 20 µm were most important then, and the smallest size fraction (< 20 µm) was growing at a significantly lower rate. However, when the latter fraction dominated (as biomass) during the summer, its doubling rates were also much higher than the > 20-µm fractions. On July 16 and 30 the daily carbon doubling-rates for the nannoplankton fraction were 1.94 and 1.63, respectively. Low doubling rates (K = 0.40) were measured on August 21, but were higher thereafter. A maximum of almost 2 doublings/day was found for the 20 to 60-µm fraction on October 15. This fraction was entirely dominated by *Skeletonema costatum*.

Assimilation Numbers

The assimilation number (mg C/mg chlorophyll *a*/h) may be used as an indicator of the growth rates of natural phytoplankton populations (Ryther and Yentsch, 1957). Because of the intrinsically higher growth rates for smaller-sized cells, a higher assimilation number might be expected to characterize them. However, this was not the case; the mean assimilation numbers for the < 20, 20 to 60 and 60 to 100-µm fractions were 3.91, 3.88, and 3.72 mg C/mg chlorophyll *a*/h, respectively; none of these differences was significant. The assimilation numbers of the different fractions were significantly different only during the winter-spring bloom (Fig. 7), when the means for the < 20-µm and > 20-µm fractions were 2.24 and 3.18, respectively – a difference significant at the 5% level. The almost complete absence of cells > 20 µm during the summer preclude similar meaningful comparisons. In the fall there is no clear pattern, partly because *Skeletonema costatum* dominated the three smaller size fractions.

The low assimilation numbers for the < 20-µm fraction during the winter-spring bloom possibly indicates that this fraction contained a lot of dead cells and detrital material. The ratio of phaeopigments to chlorophyll *a* may be taken as an indicator of such material, and in the < 20-µm fraction it was nearly always much higher than in the other fractions (Table 2). Associated with this phaeopigment would presumably be a much greater proportion of inactive chlorophyll.

Fig. 7 shows that higher assimilation numbers were found in the summer when

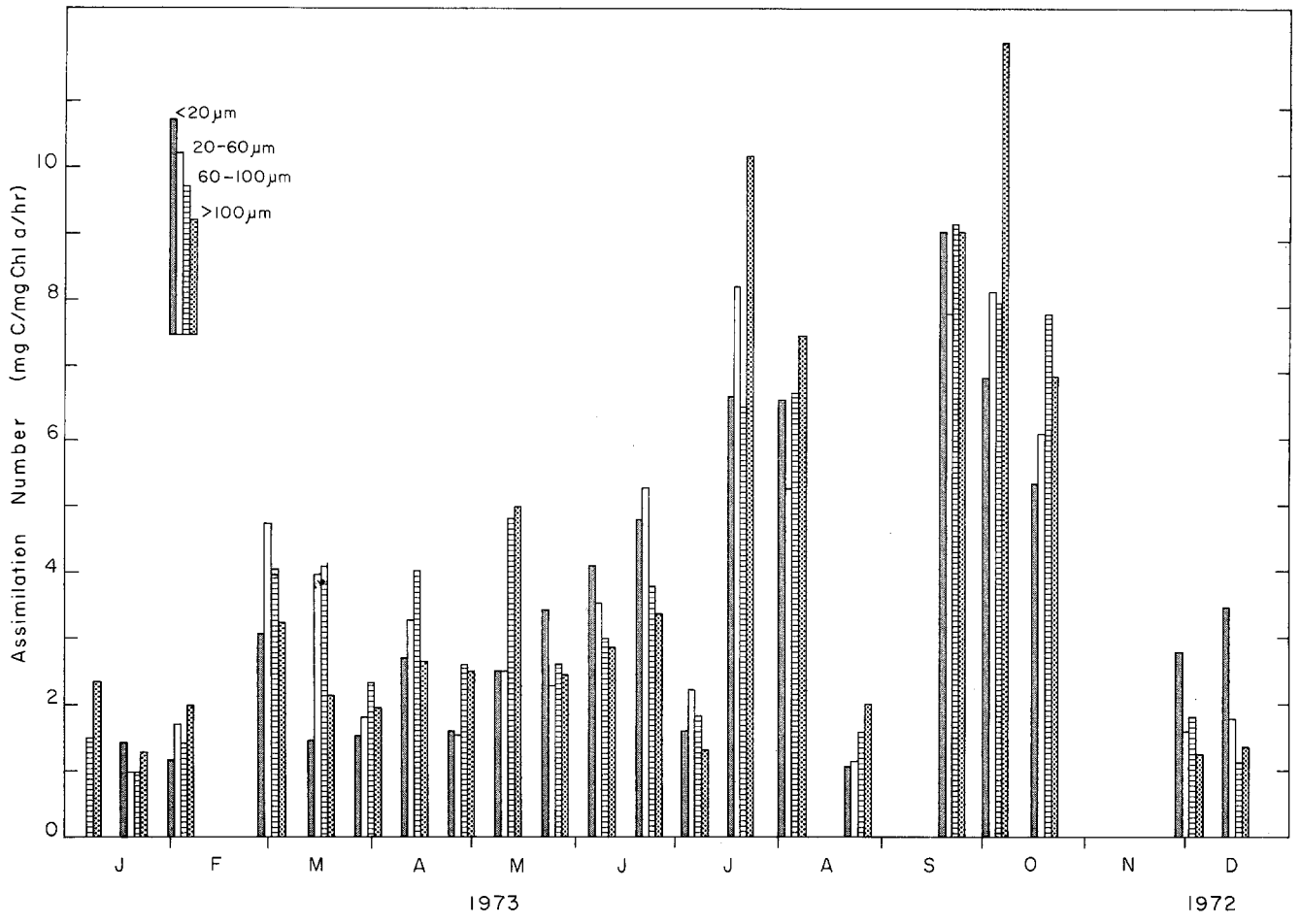

Fig. 7. Assimilation numbers (mg C/mg chlorophyll a/h) for different size fractions

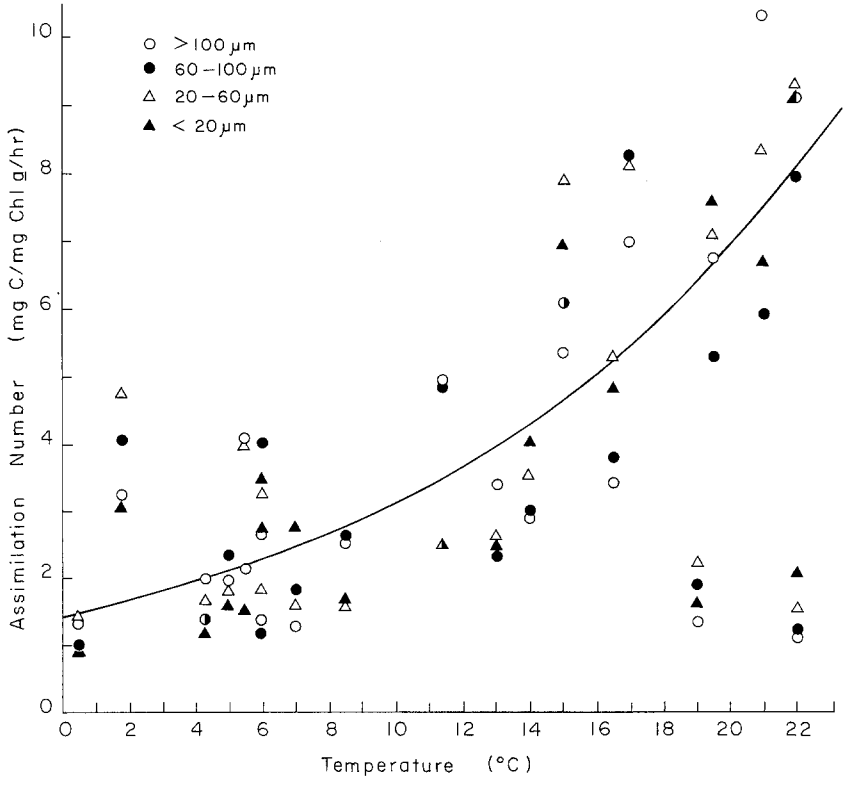

Fig. 8. Assimilation number versus temperature for different size fractions. Line is least-squares regression calculated from plot of the log of assimilation number versus temperature for all points except the two abnormally low groups at 19° and 22°C. Equation for the line is: log (assimilation no.) = 0.0348T + 0.142, where T = temperature in °C

temperatures were higher. A plot of assimilation number against temperature (Fig. 8) shows a fairly good relationship, in which the assimilation numbers increased with temperature. On July 2 and August 18, the assimilation numbers were significantly lower (groups of points at 19° and 22°C in Fig. 8), and probably indicate a nutrient-deficient population (Curl and Small, 1965). On these two days the total concentrations of urea, NH_4, NO_2 and NO_3 were 0.46 and 0.40 µg-at/l, respectively. Excluding the highly aberrant data for these two days, the relation between the log of the assimilation number and the temperature was fitted to a least squares regression: log(mg C/mg chlorophyll *a*/h) = $0.0348T + 0.142$, with a correlation coefficient of 0.79. The slope of the regression yielded a Q_{10} of 2.23.

Discussion

The spectacular and prolonged winter-spring bloom in Narragansett Bay (Smayda, 1957, 1973a, and unpublished; Pratt, 1959) is the most important event in the annual phytoplankton cycle. The domination of this bloom by long-chained diatoms suggests that the netplankters (< 20 µm) are more important than nannoplankters in the Bay. Indeed, during the 1972-1973 winter-spring bloom the netplankton was the most important fraction, contributing 77% of the biomass (as chlorophyll *a*) and 85% of the production. However, over the annual cycle, nannoplankters were approximately as equally important as the netplankters, contributing 47% of the biomass and 51% of the production. This cycle studied may perhaps be atypical because of the relative unimportance of *Skeletonema costatum* during the winter-spring bloom and the summer compared with other years (Smayda, 1957, and unpublished; Pratt, 1959). However, this cycle shows the principal features characterizing phytoplankton cycles in Narragansett Bay and northeastern coastal waters of the USA (Smayda, 1973b).

There are frequent reports that nannoplankters turn-over faster than netplankters (see Malone, 1971a), including under conditions favorable for diatom growth, such as during upwelling (Malone, 1971b). However, in the present study, when conditions were also favorable for diatom growth during the winter-spring and fall blooms, the larger fractions were not only more important in terms of biomass, but also grew more rapidly than the nannoplankters, as evidenced by both carbon doubling-rates and assimilation numbers.

These different responses may be due to several factors. The lower temperatures at which the diatoms bloomed may be one reason, since growth studies of certain small flagellates (Ukeles, 1961) showed that they did not grow well below 15°C. Nutrient uptake may also be a factor, since the half-saturation constants, K_S, and the maximum uptake rates, V_m, for nitrate and ammonia uptake vary with cell size and temperature (Dugdale, 1967; Eppley *et al.*, 1969) with the larger cells having higher values of K_S and V_m. As a result of this, higher nutrient levels might favor the growth of larger cells while the lower nutrient levels generally found during the summer might favor nannoplankton growth. Thus, the dominance of the nannoplankters and their rapid growth rates during the summer would be favored by both the high temperatures and the lower nutrient levels present then.

The fairly good direct relationship between temperature and the assimilation numbers indicates that temperature was the main factor controlling the variation in these (Fig. 8). Abnormally low assimilation numbers, which may indicate nutrient deficiency or some other "water quality" factor (Curl and Small, 1965) were found on only two occasions. Slightly lower assimilation numbers and the lower mean growth rates were found for the population occurring between the peaks of the winter-spring bloom. These suggest that the decrease in the population resulted from a decreased capacity of the water to support phytoplankton growth and was not due solely to grazing pressure. Although temperature may have little effect on the assimilation numbers of oceanic phytoplankton (Eppley, 1972), several investigators have found a relationship between assimilation numbers and temperature for estuarine phytoplankton similar to that found in the present study (Williams and Murdoch, 1966; Mandelli *et al.*, 1970). The lack of a significant nutrient effect on the assimilation numbers at most times indicates that in estuaries, including Narragansett Bay, the growth of phytoplankton is not greatly nutrient-limited, because of the rapid nutrient regeneration.

The series of short peaks in species' abundance observed poses some interesting questions. The different assimilation ratios, growth rates and changes in the C:chlorophyll *a* ratios indicate that these cycles are due to real changes in the phytoplankton growth rates rather than to scatter in ecological measurements. Rapid changes in nutrient availability, carrying capacity of the water,

and its general suitability in supporting phytoplankton growth must occur. The low nutrient levels present during the peaks in phytoplankton abundance and the high growth rates measured at these times suggest that nutrient cycling is then very rapid in lower Narragansett Bay. For example, in order to sustain the growth rate measured in the > 100-µm fraction on May 7, 2.15 µg-at N/l/day are required, if a C:N ratio of 8 is assumed. The amount of NO_3, NO_2, NH_3 and urea measured *in situ* on this date was 0.30 µg-at N/l, which would supply only a small proportion of the nitrogen needs of the phytoplankton. This gives a regeneration time for the nitrogen in the Bay of 3.4 h. On July 16 the difference is even greater; 13.0 µg-at/l/day was required by the phytoplankton and only 1.62 µg-at N/l was present, giving a regeneration time of 3.0 h.

Size fractionation of phytoplankton provides a convenient way of getting at these problems, since generally the detrital material in the fractions >20 µm is very small compared to the phytoplankton. Possibly, reliable determinations of the phytoplankton C, N, and perhaps even Si content of these fractions can be made.

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