

# Light-Saturated Photosynthesis by Phytoplankton Size Fractions in the New York Bight, USA

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## Abstract

The relationships between netplankton and nanoplankton assimilation numbers, temperature, and major nutrient concentrations were studied and evaluated in the context of seasonal patterns in the biomass of these phytoplankton size fractions. Netplankton and nanoplankton blooms typically occur during late winter (2° to 8°C) and summer (18° to 24°C), respectively. Variations in nanoplankton and netplankton assimilation numbers were not statistically related to the development or collapse of specific blooms based on weekly sampling, but assimilation numbers were higher during the bloom periods than during transition periods of rapid temperature change (8° to 18°C). Differences in the assimilation numbers between size fractions could account for the dominance of the nanoplankton fraction during the summer bloom period but not for the dominance of netplankton during the winter bloom period. Nanoplankton and netplankton assimilation numbers were exponential functions of temperature between 8° and 24°C and 8° and 20°C, respectively. Below 8°C the assimilation numbers of both fractions were higher than expected on the basis of temperature. Above 20°C netplankton assimilation numbers declined with temperature. Netplankton and nanoplankton assimilation numbers were occasionally correlated with dissolved inorganic nitrogen concentrations from less than 1.0 to more than 15  $\mu\text{g-at l}^{-1}$ . Under these conditions, nanoplankton growth rates (calculated from assimilation number and carbon:chlorophyll) were higher and increased more rapidly with dissolved inorganic nitrogen than netplankton growth rates.

## Introduction

Studies that segregate phytoplankton populations into functional ecological groups help to better understand distributions of phytoplankton production and species succession. One approach is to study the response of phytoplankton size fractions to changes in their environment (Malone, 1971a, b; Durbin *et al.*, 1975). This approach is based on observed distributions of phytoplankton size fractions (Steemann Nielsen and Jensen, 1957; Yentsch and Ryther, 1959; Teixeira, 1963; Malone, 1971c; Semina, 1972; McCarthy *et al.*, 1974) and on the theory that cell size and chain length play important roles in phytoplankton population dynamics (Paasche, 1960; Smayda, 1965; Banse, 1976) and trophic interactions (Ryther, 1969; Martin, 1970).

The residence time of phytoplankton in the euphotic zone is influenced by cell size and chain length. A number of

investigators have shown that copepods selectively graze on large particles when presented with multi-sized phytoplankton diets (Mullin, 1963; Richman and Rogers, 1969; Frost, 1972; Gaudy, 1974). High surface area-to-volume ratios facilitate suspension in stratified media (Smayda, 1970), and the distribution of phytoplankton in convection cells and upwelling systems is apparently related to particle size (Stommel, 1949; Semina, 1968; Malone, 1971a).

The parameters of growth, nutrient uptake, photosynthesis and respiration may also be influenced by cell size (Munk and Riley, 1952; Dugdale, 1967; Laws, 1975; Banse, 1976). Growth rate under certain environmental conditions appears to be inversely related to cell size (Williams, 1964; Eppley and Sloan, 1966), especially under optimal conditions (Banse, 1976). Experimental work on nitrogen-uptake kinetics by phytoplankton has led to the hypothesis that

half-saturation constants and maximum uptake velocities vary systematically with cell size in such a way that low nutrient concentrations favor the growth of small-celled species while high nutrient concentrations favor the growth of large-celled species (Dugdale, 1967; Eppley *et al.*, 1969; Parsons and Takahashi, 1973). However, evidence is accumulating which supports the view that nutritional history of phytoplankton populations is more important than cell size (Carpenter and Guillard, 1971; Caperon and Meyer, 1972; Guillard *et al.*, 1973). Laws (1975) presents a mathematical argument in favor of large-celled species having higher daily growth rates than small-celled species at low light and temperature. The validity of this argument is partially based on the assumption that specific respiration is also inversely related to cell volume, an assumption contested by Banse (1976) who concluded that existing data do not demonstrate size-dependent net growth efficiency. However, experimental observations by Taguchi (1976) indicate that  $^{14}\text{C}$ -photosynthetic efficiency (at low light intensities), respiration, and light-saturated photosynthesis are inversely related to cell size in 7 species of diatoms growing exponentially at 5° to 8°C. Field measurements also show that small phytoplankton size fractions usually have higher chlorophyll *a* specific, light-saturated photosynthesis (assimilation number) than do large size fractions (Saijo and Takasue, 1965; Malone, 1971a, b, c), although important exceptions have been reported (Durbin *et al.*, 1975).

Variations in the assimilation number should be related primarily to species composition and environmental factors which influence light-saturated growth such as temperature, nutrient supply and toxic inputs. Dinoflagellates appear to have higher assimilation numbers than diatoms (Mandelli *et al.*, 1970). Phytoplankton growing in nutrient-poor waters often exhibit low assimilation numbers relative to phytoplankton growing in nutrient-rich waters (Curl and Small, 1965; Thomas, 1970; Malone, 1971c; Thomas and Dodson, 1972), and several workers have reported relationships between assimilation numbers and temperature in estuarine or coastal waters (Williams and Murdoch, 1966; Mandelli *et al.*, 1970; Takahashi *et al.*, 1973; Durbin *et al.*, 1975; Malone, *in press a, b*). However, on the basis of available data it is difficult to determine if conditions ever exist in the oceans which favor the growth of large-celled species relative to small-celled species. The purpose of

this paper is to determine the influence of nutrient concentration and temperature on the assimilation numbers of phytoplankton size fractions and to evaluate the significance of variations in the assimilation number in terms of seasonal patterns of biomass.

#### Materials and Methods

Seasonal variations in the productivity of phytoplankton size fractions were documented on the basis of monthly observations in the lower Hudson Estuary and apex of the New York Bight from September, 1973 through August, 1974 (Malone, 1976). Maximum productivity was observed in June (2 to 6 g C m<sup>-2</sup> day<sup>-1</sup>), with a secondary peak in February (2 g C m<sup>-2</sup> day<sup>-1</sup>). Phytoplankton retained on a 22 µm Nitex screen (netplankton) dominated in February, while phytoplankton which passed the screen (nanoplankton) dominated in June. The sampling program upon which this paper is based was initiated in 1975 to study in greater temporal detail the two bloom periods and the spring transition between them. Selected stations in the Upper Bay of the lower Hudson Estuary and apex of the New York Bight (Fig. 1) were monitored at approximately weekly intervals from April through July, 1975, February through March, 1976 and in November, 1975. Samples were collected from 3 to 5 depths, depending on the depth of the water column which ranged from 10 m in the Upper Bay to 20-30 m in the apex. All sampling was conducted during the day between 2 h after sunrise and 2 h before sunset.

Nanoplankton and netplankton chlorophyll *a* concentrations were measured by fluorometry (Strickland and Parsons, 1972) following serial fractionation through 22 µm mesh Nitex screens and Gelman type AE glass-fiber filters. Comparison of the sum of netplankton and nanoplankton fractions with unfrac-tionated samples gave a coefficient of variation of 12%. Particulate organic carbon (POC) was measured by combustion in oxygen with a Coleman Model 33 CH analyzer.

The photosynthetic production of particulate organic carbon by nanoplankton and netplankton fractions was estimated from  $^{14}\text{C}$  uptake measurements. Light-saturated photosynthetic rates (photosynthetic capacity) were determined from 2 h incubations in fluorescent light incubators. Samples collected from 1 to 3 m below the surface were inoculated with 5 µCi  $^{14}\text{C}$  labelled bicarbonate and

incubated at surface-water temperature under light intensities of 0.10, 0.06, 0.03, 0.015 and 0.005 cal cm<sup>-2</sup> min<sup>-1</sup>. Light saturation was observed at 0.06 or 0.10 cal cm<sup>-2</sup> min<sup>-1</sup>, and no obvious seasonal trends were found.

Assimilation numbers (AN) were calculated by dividing photosynthetic capacity by corresponding chlorophyll a concentrations. *In situ* primary productivity was estimated using sunlight incubators in combination with neutral density filters which simulated the percent light depths (estimated from Secchi disc measurements) from which samples were collected (100, 60, 30, 15 and 5%). Samples were incubated for 24 h at surface-water temperature. Following both artificial light and sunlight incubations, the samples were fractionated by serial filtration through 22 μm Nitex screens and HA Millipore filters. The screens and filters were washed with particle-free seawater, placed over fuming HCl for 30 sec, dried in a CO<sub>2</sub>-free atmosphere, and their activity measured with a liquid scintillation counter. Mean coefficients of variation between duplicate light bottles were 16 ± 5% and 8 ± 4% (95% confidence limit) for netplankton and nanoplankton fractions, respectively. The regression of measured netplankton photosynthetic capacity (PC = direct measure of activity on the 22 μm mesh screens) on calculated netplankton photosynthetic capacity (PC' = unfractionated -nanoplankton) was  $PC = 0.91 PC' + 0.72$  ( $r = 0.97$ ,  $DF = 128$ ). The regression coefficient was significantly less than 1.00 (95% CL = ± 0.05), but the intercept was not significantly different from 0 (95% CL = ± 1.18). Measured netplankton PC tended to be slightly greater than calculated values when PC was less than 8 μg C l<sup>-1</sup> h<sup>-1</sup>, and slightly less than calculated values when greater than 8 μg C l<sup>-1</sup> h<sup>-1</sup> (range of 0.1 to 185 μg C l<sup>-1</sup> h<sup>-1</sup>, with 46% of the PC values less than 8.0 and 96% less than 50.0). However, this systematic error is not significant ( $P < 0.05$ ) at PC' values less than 50.0 μg C l<sup>-1</sup> h<sup>-1</sup>.

Temperature was measured with protected reversing thermometers, and dissolved inorganic nutrient analyses were performed with a Technicon AAI three-channel autoanalyzer using standard Technicon procedures (Strickland and Parsons, 1972). Each method was calibrated and checked for linear response during a series of replicate standards run at the beginning and at 30 sample intervals during each run. Precision was ± 0.25 μg-at l<sup>-1</sup> or better for all methods.

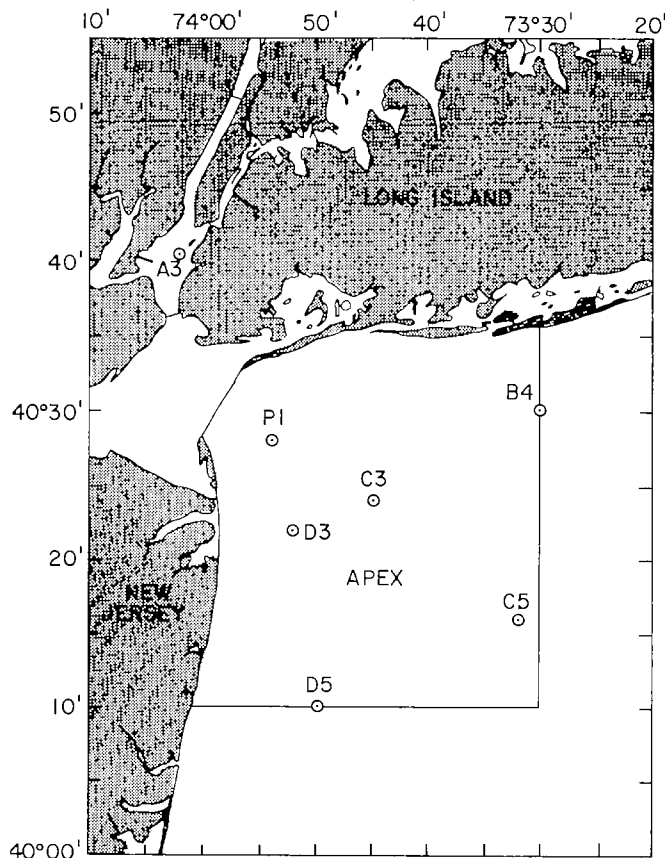


Fig. 1. Station locations in Upper Bay (A3) of the lower Hudson Estuary and the apex of the New York Bight

## Results and Discussion

### Temperature and Nutrients

Surface temperature ranged from a February minimum of 2.0°C to a July maximum of 23.4°C (Fig. 2). Geographic ranges of surface temperature were usually less than 2°C. During the summer, the water column was well stratified, with a thermocline located between 5 and 15 m below the surface in the apex. Thermal stratification was poorly developed during late fall and winter, and vertical profiles were often characterized by thermal inversions during the winter. Based on these and earlier observations (Malone, 1976), the hydrographic regime of the apex can be divided into 4 seasons. Surface temperatures are low (less than 8°C) and relatively constant during the winter (January - March) and high (above 19°C) and relatively constant during the summer (June - August). Spring and fall can be considered transition periods. During the spring, surface temperatures increase rapidly (9°C to 18°C in May) as the water column becomes

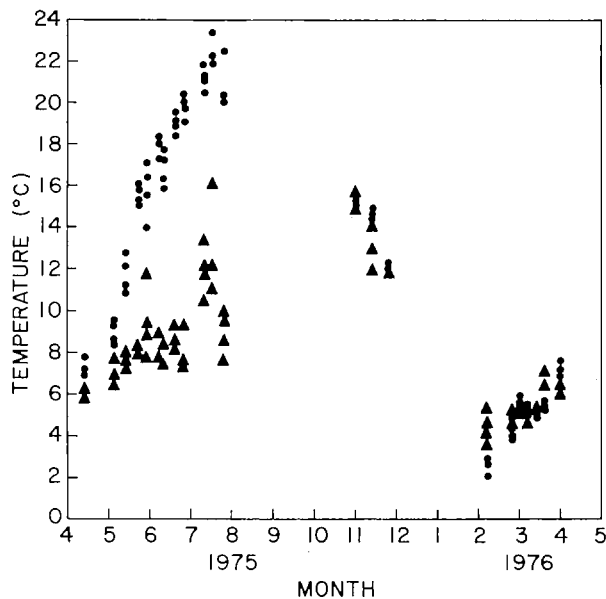


Fig. 2. Surface (circles) and bottom (triangles) temperature at Stations C3, C5, D3 and D5 in the apex of the New York Bight

Table 1. Mean, range and coefficient of variation (C) for major nutrient concentrations, their atomic ratios, and salinity during June-July, 1975 and February-March, 1976 in the apex of the New York Bight (exclusive of Station P1)

Property	June-July			February-March		
	Mean	Range	C (%)	Mean	Range	C (%)
NO <sub>3</sub> -N	3.6	0.1-17.4	119	3.6	0.8-11.2	68
NH <sub>4</sub> -N	0.7	0.0- 4.5	141	1.9	0.6- 4.2	55
PO <sub>4</sub> -P	0.6	0.4- 1.3	38	1.0	0.5- 1.8	30
SiO <sub>4</sub> -Si	5.2	0.6-16.5	97	3.5	0.7- 8.5	60
N:P	7.3	1 -29	111	5.6	1 -16	60
N:Si	0.9	0.1-33.0	73	1.8	0.8- 4.4	37
Salinity (‰)	29.9	26.2-31.5	5	29.8	25.6-31.2	5

Table 2. Mean primary productivity (g C m<sup>-2</sup> day<sup>-1</sup>), mean photic zone chlorophyll *a* (µg l<sup>-1</sup>) and associated coefficients of variation (C) for nanoplankton and netplankton fractions in the Upper Bay of the lower Hudson Estuary and the apex of the New York Bight during the two major bloom periods

	Productivity		Chlorophyll <i>a</i>	
	Upper Bay	Apex	Upper Bay	Apex
<b>June-July</b>				
Nanoplankton	0.73	1.22	2.87	4.03
C (%)	89	129	105	109
Netplankton	0.06	0.35	0.28	1.39
c (%)	97	108	86	108
<b>Feb.-March</b>				
Nanoplankton	0.08	0.46	2.20	1.47
C (%)	33	61	24	53
Netplankton	0.20	0.93	5.87	5.73
C (%)	27	34	28	50

stratified. The process is reversed during the fall as surface water temperatures decline and thermal stratification breaks down.

The supply of nutrients to the euphotic zone is continuous and unrelated to the seasonal cycle of water column stratification except to the extent that temperature influences regeneration rates and thermal stratification tends to restrict nutrient-rich estuarine water to the surface layer (Garside *et al.*, 1976; Malone, 1976). Surface nutrient concentrations in the Upper Bay were always high as a consequence of the discharge of sewage wastes from the New York-New Jersey metropolitan region (Simpson *et al.*, 1975; Garside *et al.*, 1976). Dissolved inorganic nitrogen (DIN = nitrate + nitrite + ammonia) and silicate concentrations were always above 10 µg-at l<sup>-1</sup>, and N:P ratios (atomic) fluctuated between 10 and 50. Surface nutrient concentrations in the apex of the New York Bight were lower than in the Estuary and generally decreased with distance from the mouth of the Estuary (Malone, 1976). Surface concentrations in the apex were most variable during late spring and summer when the water column was stratified (Table 1). Nitrate, ammonia and phosphate tended to be higher and silicate lower during the winter than during late spring and summer. N:P ratios were less than 10 except when DIN exceeded 5 µg-at l<sup>-1</sup>.

#### Carbon Production and Biomass

Phytoplankton productivity ranged from 0.01 to 2.31 g C m<sup>-2</sup> day<sup>-1</sup> (200 g C m<sup>-2</sup> year<sup>-1</sup>) in the Upper Bay and from 0.10 to 6.59 g C m<sup>-2</sup> day<sup>-1</sup> (480 g C m<sup>-2</sup> year<sup>-1</sup>) in the apex of the New York Bight. Netplankton accounted for an average of 25% of the productivity and 36% of the chlorophyll *a* (euphotic zone) in the Upper Bay compared to 42% of the productivity and 52% of the chlorophyll *a* in the apex. High productivity and clear dominance of one size fraction over the other occurred during the winter (2°C to 8°C) and summer (19°C to 24°C) periods when temperature was relatively constant. Nanoplankton accounted for a mean of 92% of the productivity in the Upper Bay and 78% in the apex during June and July, while netplankton accounted for 71% in the Bay and 67% in the apex during February and March (Table 2). During the June-July period of nanoplankton dominance, productivity in the apex varied from 0.5 to 6.6 g C m<sup>-2</sup> day<sup>-1</sup> compared to 0.5 to 2.3 g C m<sup>-2</sup> day<sup>-1</sup> during the February-March period of net-

plankton dominance. Increases in mean euphotic zone (MPZ) chlorophyll a above  $5 \mu\text{g l}^{-1}$  were caused by nanoplankton during June and July (Fig. 3) and by netplankton during February and March (Fig. 4). MPZ chlorophyll a tended to be higher and chlorophyll a specific productivity (based on integrated euphotic zone values) lower during the winter period than during the summer period. The high degree of heterogeneity in the distribution of chlorophyll a during the June-July period compared to February-March (Table 2) probably reflects higher growth rates relative to mixing rates during the summer.

Variations in POC were significantly ( $P < 0.05$ ) correlated with chlorophyll a when concentrations of chlorophyll a exceeded  $5 \mu\text{g l}^{-1}$ . Two regressions were found corresponding to temperatures above (1) and below (2)  $8^\circ\text{C}$ :

$$\text{POC} = 43 + 72 \text{ Chl} \quad (r = 0.97, \text{DF} = 30) \quad (1)$$

$$\text{POC} = 355 + 46 \text{ Chl} \quad (r = 0.96, \text{DF} = 12) \quad (2)$$

where POC =  $\mu\text{g C l}^{-1}$  and Chl =  $\mu\text{g chlorophyll a liter}^{-1}$ . A similar seasonal trend in the regression coefficient has been found in Narragansett Bay (Furnas, personal communication). These ratios (regression coefficient = carbon:chlorophyll a) are used to calculate carbon-specific growth rates from light-saturated, chlorophyll a specific photosynthesis (2 h incubations). The high y-intercept corresponding to temperatures below  $8^\circ\text{C}$  suggests higher background levels of organic detritus during the winter compared to warmer seasons.

Small pigmented flagellates and chlorophytes with spherical diameters of less than  $10 \mu\text{m}$  were numerically most abundant during nanoplankton blooms. Netplankton blooms were dominated by *Skeletonema costatum* and *Nitzschia seriata*, with *Thalassiosira nordenskiöldii*, *Rhizosolenia setigera*, *Detonula* sp. and *Asterionella japonica* sporadically abundant. Dinoflagellates are not usually abundant at this time of year (Malone, 1976; Hulburt, personal communication). However, the abundance of *Ceratium tripos* increased from 1 to  $10 \times 10^3 \text{ cells l}^{-1}$  in late February to  $10$  to  $50 \times 10^3 \text{ l}^{-1}$  by the end of March.

The extreme dominance of *Ceratium tripos* by this time (over 90% of total cells at Stations C5 and D5) allowed the chlorophyll a and POC content of *C. tripos* cells to be calculated from netplankton chlorophyll a and POC concentrations. Chlorophyll a ranged from 0.089 to 0.100 ng cell $^{-1}$  (mean = 0.093) and POC from 0.021 to 0.026  $\mu\text{g cell}^{-1}$  (mean = 0.0255). Based on mean cellular chlorophyll a, *C. tripos* accounted for 2 to 30% (mean = 22%) of netplankton chlorophyll a during

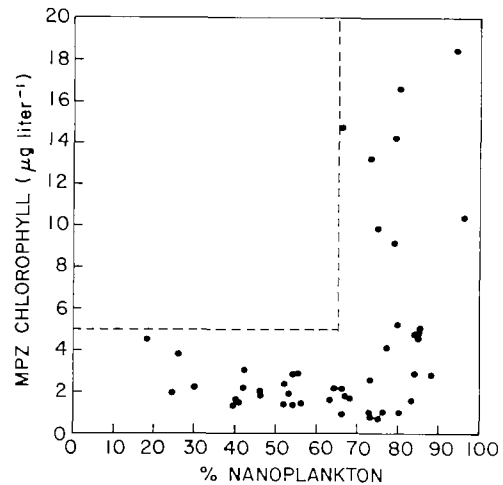


Fig. 3. Mean euphotic zone (MPZ) chlorophyll a concentration as a function of proportion of nanoplankton chlorophyll a from May through July, 1975

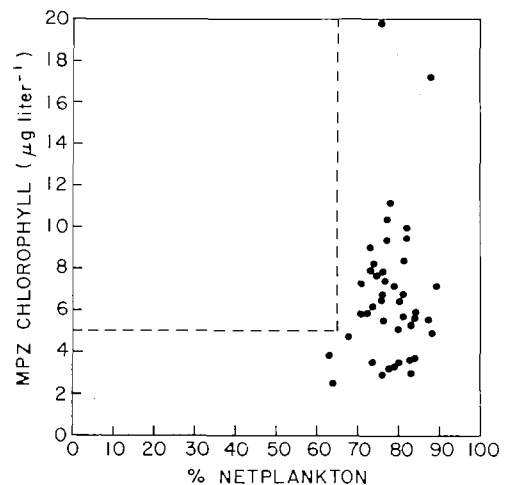


Fig. 4. Mean euphotic zone (MPZ) chlorophyll a concentration as a function of proportion of netplankton chlorophyll a from February through March, 1976

February and March, except at the end of March when it accounted for 15 to 100% (mean = 55%) of netplankton chlorophyll a. Netplankton blooms (MPZ chlorophyll a greater than  $5 \mu\text{g l}^{-1}$ ) were characterized by low proportions of *C. tripos* (less than 10%). The proportion of *C. tripos* (% chlorophyll) was significantly correlated ( $r = 0.91, P < 0.01$ ) with the C:chlorophyll ratio of the netplankton fraction. The regression equation  $\% \text{ chlorophyll} = 0.436 \text{ C:chlorophyll} - 21.36$  yields a C:chlorophyll ratio for *C. tripos* of 278 and a C:chlorophyll ratio for diatoms of 49. The latter is consistent

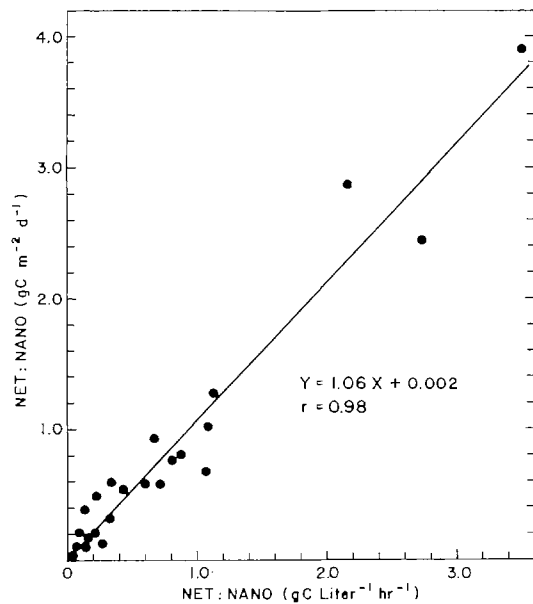


Fig. 5. Netplankton:nanoplankton ratio of primary productivity as a function of net:nano ratio of photosynthetic capacity

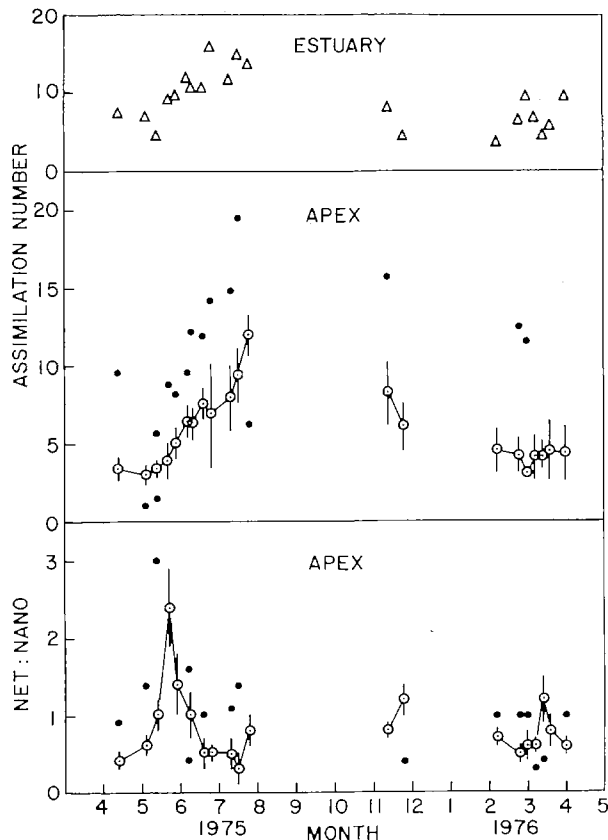


Fig. 6. Phytoplankton assimilation numbers [ $\text{g C (g chlorophyll} \cdot \text{h)}^{-1}$ ] and netplankton:nanoplankton assimilation number ratios. Mean values  $\pm 1$  SD are given for the apex (ringed dots) and assimilation numbers which were not used to calculate the means are indicated (filled circles)

Table 3. Mean photosynthetic capacity ( $\text{PC} = \mu\text{g C l}^{-1} \text{h}^{-1}$ ;  $n = 6$ ; Stations A3, P1, C3, C5, D3 and D5), coefficient of variation (C) and proportion of spatial variance in PC reduced by chlorophyll *a* ( $r^2$ )

Date	Nanoplankton			Netplankton		
	PC	C(%)	$r^2$	PC	C(%)	$r^2$
1975						
21 Apr.	10.0	89	0.93	15.1	146	0.98
4 May	7.3	135	0.97	3.7	89	0.89
13 May	11.6	78	0.73	6.8	95	0.97
20 May	34.3	88	0.29 <sup>a</sup>	12.0	75	0.98
27 May	18.0	85	0.88	4.0	80	0.94
6 June	39.5	106	0.92	7.7	92	0.95
10 June	24.6	114	0.96	23.2	149	0.99
18 June	33.4	130	0.99	7.1	130	0.94
24 June	24.2	91	0.90	5.4	74	0.33 <sup>a</sup>
10 July	42.9	90	0.74	4.2	105	0.82
16 July	44.4	172	0.99	2.6	101	0.68
25 July	77.9	95	0.89	19.2	77	0.96
13 Nov.	15.2	79	0.86	9.7	97	0.69
24 Nov.	7.4	48	0.94	8.2	62	0.46 <sup>b</sup>
1976						
7 Feb.	3.7	52	0.72	7.8	29	0.23 <sup>c</sup>
22 Feb.	16.2	85	0.87	37.0	104	0.80
1 Mar.	17.9	74	0.42 <sup>a</sup>	57.9	115	0.95
6 Mar.	11.5	44	0.80	27.8	47	0.58
14 Mar.	6.4	22	0.01 <sup>c</sup>	16.8	23	0.04 <sup>c</sup>
20 Mar.	10.1	49	0.72	19.7	38	0.19 <sup>a</sup>
31 Mar.	17.7	110	0.89	30.0	92	0.57

<sup>a</sup>Stepwise multiple-regression analysis of assimilation number ( $\text{PC chlorophyll}^{-1}$ ) on dissolved inorganic nitrogen, silicate, salinity and temperature (Stations P1, C3, C5, D3 and D5) indicates that growth may have been nitrogen-limited.

<sup>b</sup>Spatial variations in PC positively correlated ( $r = 0.75$ ,  $n = 6$ ) with salinity

<sup>c</sup>Spatial distributions of PC and the assimilation number were uniform (C less than 30%)

with the value of 46 derived from the POC-chlorophyll regression for this period.

#### Photosynthetic Capacity and Assimilation Number

Netplankton:nanoplankton ratios of primary productivity ( $\text{g C m}^{-2} \text{day}^{-1}$ ) were significantly correlated ( $P < 0.01$ ) with net:nano ratios of photosynthetic capacity ( $\text{g C l}^{-1} \text{h}^{-1}$ ) (Fig. 5). The regression coefficient and  $y$ -intercept were not significantly different from 1 and 0, respectively. Incubation time did not influence the relative importance of the two size fractions, and photosynthetic

capacity was a good index of their relative photosynthesis in the euphotic zone.

With few exceptions, spatial variations in netplankton and nanoplankton photosynthetic capacity were significantly ( $P < 0.05$ ) correlated with concurrent variations in the chlorophyll *a* content of each size fraction (Table 3). Spatial variations in netplankton and nanoplankton assimilation numbers (AN) were small ( $C < 50\%$ ) and unrelated to major nutrient concentrations on most occasions. This was observed even though DIN and  $SiO_4$  concentrations ranged from greater than  $15 \mu\text{g-at l}^{-1}$  in the Upper Bay to less than  $1.0 \mu\text{g-at l}^{-1}$  in the apex.

The seasonal cycle of phytoplankton AN was similar to that observed in 1973-1974 when AN were found to be exponentially related to temperature above  $8^\circ\text{C}$  (Malone, in press a). AN increased from less than  $5 \text{ g C (g chlorophyll} \cdot \text{h)}^{-1}$  in April to greater than 10 in July, decreased during the fall, and fluctuated around 5 during the winter (Fig. 6).

Temporal variations in nanoplankton and netplankton AN were not related to the occurrence of blooms except in the sense that AN were higher during the bloom periods than during the transition periods of rapid temperature change. Netplankton AN were typically equal to or less than nanoplankton AN most of the year (Fig. 6). Paradoxically, netplankton:nanoplankton ratios of AN were highest in the apex during the transition between the periods of netplankton and nanoplankton dominance. Maximum net:nano ratios occurred in late May ( $15^\circ$  to  $16^\circ\text{C}$ ) coincident with the first peak in a series of nanoplankton blooms which characterized the summer period.

Both nanoplankton and netplankton AN were exponential functions of temperature, although the temperature relationships of the two fractions were different. Nanoplankton AN increased exponentially with temperature from  $8^\circ$  to  $24^\circ\text{C}$  with different relationships for estuarine and apex populations (Fig. 7). Netplankton AN were also exponentially related to temperature, but estuarine and apex populations exhibited similar temperature relationships between  $8^\circ$  and  $20^\circ\text{C}$ , so the data were pooled (Fig. 8).

Temperature coefficients for the nanoplankton fraction (estuary,  $Q_{10} = 2.6$ ; apex,  $Q_{10} = 2.0$ ) were close to the theoretical value to 2.3 in contrast with the high netplankton  $Q_{10}$  (4.0). This suggests that the nanoplankton fraction may consist of species which are physiologically more homogeneous than the species which comprise the netplankton fraction. For example, Mandelli

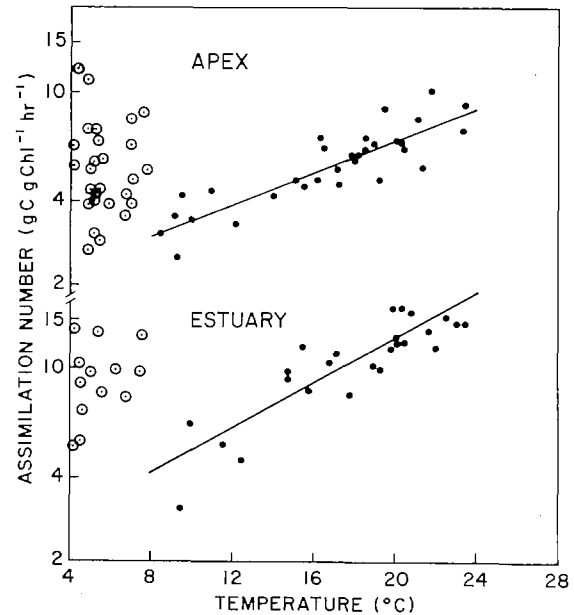


Fig. 7. Nanoplankton assimilation numbers as a function of temperature ( $T$ ) in the apex ( $\log_{10} \text{AN} = 0.029 T + 0.241$ ,  $r = 0.84$ ) and the estuary ( $\log_{10} \text{AN} = 0.041 T - 0.288$ ,  $r = 0.88$ ). Regression equations were calculated from measurements made from April through November, 1975 (filled circles). Measurements during February and March, 1976 (ringed dots) were higher than expected on basis of the temperature functions

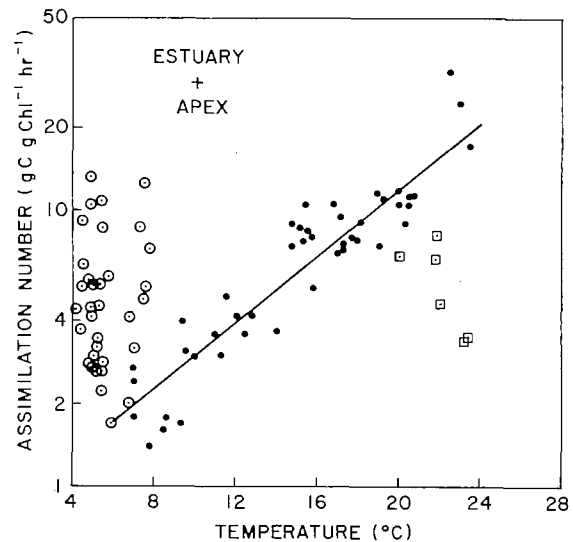


Fig. 8. Netplankton assimilation numbers as a function of temperature in the apex and estuary ( $\log_{10} \text{AN} = 0.060 T - 0.130$ ,  $r = 0.92$ ). Regression equations were calculated from measurements made from April through November, 1975 (filled circles), except for measurements at temperatures above  $20^\circ\text{C}$  in the apex (boxed dots). Measurements during February and March, 1976 (ringed dots) were higher than expected on basis of the temperature function

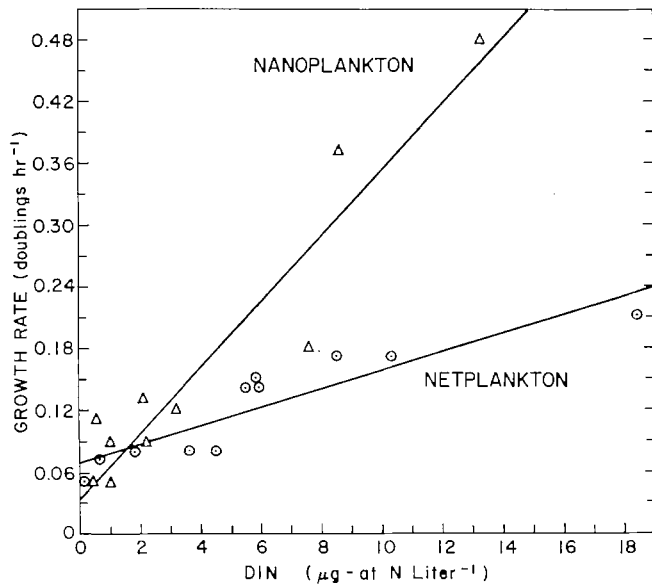


Fig. 9. Carbon-specific nanoplankton (triangles) and netplankton (ringed dots) growth rates as functions of DIN. Based on data from 20 May and 1 March for nanoplankton and 24 June and 20 March for netplankton (nanoplankton  $\mu_m = 0.031 \text{ DIN} + 0.042$ ,  $r = 0.95$ ; netplankton  $\mu_m = 0.009 \text{ DIN} + 0.068$ ,  $r = 0.96$ )

et al. (1970) found that diatoms dominated the netplankton off southern Long Island in February and March while dinoflagellates dominated from April through August, 1966. *Skeletonema costatum* dominated in February, *Thalassiosira* sp. and *Chaetoceros* sp. in March, *Peridinium depressum* in April, *Ceratium massiliense* in May and *Ceratium tripos* from June through August. Mandelli et al. also observed that AN were increasing functions of temperature, with AN being higher when dinoflagellates dominated than when diatoms dominated, especially at temperatures above 15°C. Thus, the high  $Q_{10}$  found for the netplankton fraction probably reflects the photosynthetic capacity of a succession of species, and temperature coefficients derived from field measurements, such as those reported on here, should be considered a community characteristic.

Below 8°C, AN for both fractions were higher than expected on the basis of temperature (Figs. 7 and 8), a phenomenon which was observed during the netplankton bloom period in 1974 (Malone, in press a). This could be a consequence of selection for species adapted to photosynthesize rapidly at low temperatures or temperature acclimation during the cold-water period by species such as *Skeletonema costatum* (Jørgensen, 1968).

Above 20°C, netplankton AN continued to increase with temperature in the Upper Bay and Station P1, but declined with temperature in the apex. A Wilcoxon signed rank test performed on pooled AN from June through July showed that netplankton AN were higher ( $P < 0.05$ ) in the Upper Bay than in the apex. Takahashi et al. (1973) observed a similar decline in phytoplankton AN at temperatures greater than 15°C in the Fraser River Estuary and concluded that photosynthesis was nutrient-limited at higher temperatures. This did not appear to be the case in the apex, where residual DIN and  $\text{SiO}_4$  ( $> 1.0 \mu\text{g-at l}^{-1}$ ) were observed throughout the period when temperatures were greater than 20°C, and variations in netplankton AN were not related to nutrient concentrations. However, since inhibition was not found in the Upper Bay where netplankton populations are derived primarily from the apex (Malone, in press b), the decline above 20°C was probably not temperature inhibition *per se*, but an effect related to factors other than major nutrient concentrations and temperature.

Nanoplankton AN were highest (Wilcoxon signed-rank test,  $P < 0.05$ ) in the Upper Bay regardless of season, but no statistical difference between stations was found for netplankton AN during February-March. If AN are an index of light-saturated phytoplankton growth rates, it appears that estuarine water is a better growth medium than coastal water for nanoplankton species throughout the year and for netplankton species during the summer.

Poor correlations between photosynthetic capacity and chlorophyll a were occasionally observed (Table 3). Stepwise multiple regression analysis of AN on temperature, salinity, DIN,  $\text{SiO}_4$  and  $\text{PO}_4$  ranked DIN as the most important variable on 20 May and 1 March for nanoplankton and on 24 June and 20 March for netplankton. Regressions of carbon-specific growth rates (calculated from AN and appropriate C:chlorophyll ratios) on DIN were highly significant ( $P < 0.01$ ) and independent of season (Fig. 9). Nanoplankton growth rates were higher and increased more rapidly with DIN than netplankton growth rates. These relationships were observed over the same range of DIN concentrations ( $< 1.0$  to  $20 \mu\text{g-at l}^{-1}$ ) for which no nutrient effect could be shown. This suggests that transient nutrient-limited growth can occur in the apex as a consequence of changes in nutrient supply rates and that growth rates can be independent of DIN concentrations to less than  $1.0 \mu\text{g-at l}^{-1}$ .



Table 4. Nanoplankton and netplankton assimilation numbers (AN) calculated from temperature ( $T$ ) functions for the apex (nanoplankton,  $\log_{10} \text{AN} = 0.029 T + 0.241$ ; netplankton  $\log_{10} \text{AN} = 0.060 T - 0.130$ ) and carbon-specific growth rates ( $\mu_m = \text{doublings h}^{-1}$ ) calculated from the AN and derived C:chlorophyll ratios compared to maximum cell-division rates in both culture (Eppley, 1972) and continuous culture (Goldman and Carpenter, 1974)

$T$ ( $^{\circ}\text{C}$ )	C:chloro- phyll	AN		$\mu_m$		Batch	Continuous
		Nano	Net	Nano	Net		
5	46	2.4 (6.2) <sup>a</sup>	1.5 (4.8) <sup>a</sup>	0.07 (0.18) <sup>c</sup>	0.05 (0.14) <sup>c</sup>	0.12	0.03
10	72	3.4	3.0	0.07	0.06	0.16	0.06
15	72	4.7	5.9	0.09	0.11	0.22	0.09
20	72	6.6	11.7	0.13	0.22	0.30	0.13
25	72	9.2	23.4 (1.3) <sup>b</sup>	0.17	0.41 (0.03) <sup>c</sup>	0.41	0.19

<sup>a</sup>Mean assimilation number for all measurements below 8 $^{\circ}\text{C}$ .

<sup>b</sup>Mean assimilation number for all measurements above 20 $^{\circ}\text{C}$ .

<sup>c</sup>Growth rate calculated from corresponding mean assimilation number.

### Conclusions

Nutrient supply to the apex of the New York Bight is continuous and related primarily to estuarine runoff and regeneration rates (Garside *et al.*, 1976; Malone, in press a). Although DIN concentrations varied from 0.1 to greater than 15  $\mu\text{g-at l}^{-1}$ , netplankton and nanoplankton AN rarely exhibited nutrient responses such as those described by Curl and Small (1965) and Malone (1971c). Thomas and Dodson (1972) found that AN were related to dilution rate in nitrogen-limited chemostats, and steady-state growth rates are typically independent of detectable nutrient concentration in continuous-flow cultures (cf. Caperon and Meyer, 1972). To the extent that AN are indicative of light-saturated growth rates, nutrient supply rates to the apex must be equal to or greater than phytoplankton demand over periods which are long enough to prevent sustained nutrient depletion and consequent changes in cell nutrient quotas and growth rates.

Seasonal cycles of netplankton and nanoplankton productivity and biomass were out of phase, netplankton blooms occurring during the period of low and relatively constant temperature and nanoplankton blooms occurring during the period of high and relatively constant temperature. High AN did not precede blooms, nor did low AN coincide with their demise. Since C:chlorophyll ratios appeared to be relatively constant during the two bloom periods, the development and termination of netplankton and nanoplankton blooms in the apex were

probably related to factors other than changes in growth potential, e.g. sinking, grazing or physical processes which seed, concentrate or dilute phytoplankton.

In an effort to better understand changes in the biomass of one fraction relative to the other, carbon-specific growth rates (growth potential =  $\mu_m$ ) were calculated from Eppley's (1972) Eq. (5). Netplankton and nanoplankton  $\mu_m$  are compared with values predicted by the temperature functions derived from batch-culture experiments by Eppley (1972) and from continuous-culture experiments by Goldman and Carpenter (1974) (Table 4). From 10 $^{\circ}\text{C}$  to 25 $^{\circ}\text{C}$  nanoplankton  $\mu_m$  in the apex is predicted best by the continuous-culture function. Netplankton  $\mu_m$  falls between the two functions, being equal to that predicted by the continuous-culture function at 10 $^{\circ}\text{C}$ , and equal (Upper Bay only) to that predicted by the batch-culture function at 25 $^{\circ}\text{C}$ . The  $\mu_m$  of both fractions were higher at 5 $^{\circ}\text{C}$  than predicted by any of the temperature functions, a phenomenon which has been documented by Goldman and Ryther (in press) for *Skeletonema costatum* in continuous culture. It appears that differences in  $\mu_m$  cannot account for the dominance of netplankton during the cold-water period. However, these data must be interpreted with care since solitary and double cells of *S. costatum* were frequently abundant in the nanoplankton fraction during netplankton blooms.

The temperature inhibition effect found for netplankton in the apex at temperatures above 20 $^{\circ}\text{C}$  could provide a

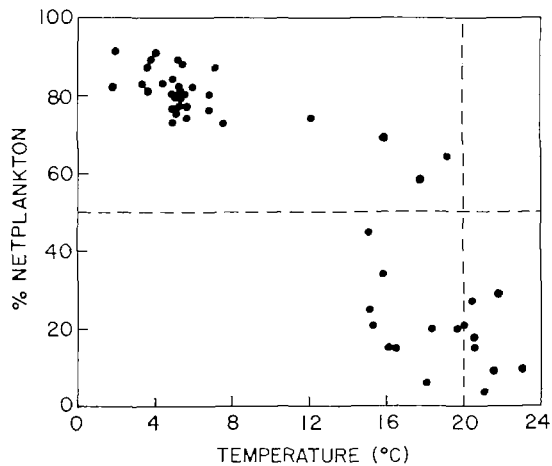


Fig. 10. Variations in percent of netplankton chlorophyll *a* with surface temperature in the euphotic zone when mean euphotic zone chlorophyll *a* exceeded  $5 \mu\text{g l}^{-1}$  (data from 1973-1974 and 1975-1976)

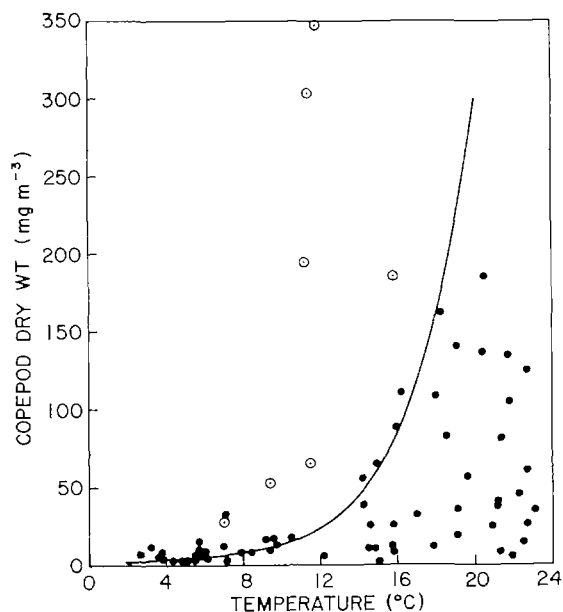


Fig. 11. Variations in copepod dry weight with temperature (from Chervin, unpublished data). Ringed dots: fall 1973; filled circles: all remaining data from 1973-1974 and 1975-1976

partial explanation of the dominance of nanoplankton during the warm-water period. Increases in nanoplankton relative to netplankton during summer blooms could be a consequence of higher nanoplankton growth rates in the apex. However, this could not have been the case in the Upper Bay where the temperature inhibition effect was not observed, and netplankton growth rates were much higher than nanoplankton growth rates. Here, selective removal or seeding must favor

the nanoplankton fraction during the summer.

Nanoplankton  $\mu_m$  was better predicted by the temperature function derived from continuous cultures than by that derived from batch cultures, while netplankton  $\mu_m$  at high temperatures in the Upper Bay was better predicted by the batch-culture temperature function (Table 4). During the warm-water period, nanoplankton dominate the phytoplankton in the Upper Bay, and netplankton appear to be derived mainly from the apex via upstream transport of bottom water (Malone, in press b). The residence time of netplankton in the euphotic surface layer must be short, and netplankton populations are probably restocked by mixing between the surface and bottom layers. Thus, it is conceivable that netplankton inoculated into the nutrient-rich, euphotic surface layer undergo a short burst of exponential growth analogous to that observed in high-temperature ( $20^\circ$  to  $25^\circ\text{C}$ ) batch cultures (Eppley, 1972).

The transition from netplankton- to nanoplankton-dominated blooms took place during May and June when the surface temperature increased from  $15^\circ$  to  $20^\circ\text{C}$  (Fig. 10). While netplankton  $\mu_m$  was higher than nanoplankton  $\mu_m$  between  $15^\circ$  and  $20^\circ\text{C}$  (Table 4), the majority of blooms were dominated by nanoplankton. Again, the fact that netplankton did not dominate blooms in the apex during this period indicates that netplankton populations were selectively removed or diluted relative to nanoplankton populations. Copepod grazing may provide at least a partial explanation. Pooled data from 1973-1974 and 1975-1976 (Chervin, unpublished data) indicate that peak heights in copepod biomass increased exponentially with surface temperature, the maximum slope occurring between  $15^\circ$  and  $20^\circ\text{C}$  (Fig. 11). These variations suggest a seasonal pattern of copepod grazing pressure characterized by a winter minimum corresponding to the netplankton bloom period and an exponential increase during late spring culminated by high grazing pressure during early summer. If netplankton populations are selectively grazed in proportion to copepod biomass (which usually accounted for more than 70% of the zooplankton captured by a  $202 \mu\text{m}$  mesh net), the decline in netplankton between  $15^\circ$  and  $20^\circ\text{C}$  could have been a consequence of a rapid increase in grazing pressure.

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#### Literature Cited

- Banse, K.: Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size - a review. *J. Phycol.* 12, 135-140 (1976)
- Caperon, J. and J. Meyer: Nitrogen-limited growth of marine phytoplankton - II. Uptake kinetics and their role in nutrient limited growth of phytoplankton. *Deep-Sea Res.* 19, 619-632 (1972)
- Carpenter, E.J. and R.R. Guillard: Intraspecific differences in nitrate half-saturation constants for three species of marine phytoplankton. *Ecology* 52, 183-185 (1971)
- Curl, H. and L.F. Small: Variations in photosynthetic assimilation ratios in natural, marine phytoplankton. *Limnol. Oceanogr.* 10 (Suppl.), R67-R72 (1965)
- Dugdale, R.C.: Nutrient limitation in the sea: dynamics, identification and significance. *Limnol. Oceanogr.* 12, 685-695 (1967)
- Durbin, E.G., R.W. Krawiec and T.J. Smayda: Seasonal studies on the relative importance of different size fractions of phytoplankton in Narragansett Bay (USA). *Mar. Biol.* 32, 271-287 (1975)
- Eppley, R.W.: Temperature and phytoplankton growth in the sea. *Fish. Bull. U.S.* 70, 1063-1085 (1972)
- , J.N. Rogers and J.J. McCarthy: Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. *Limnol. Oceanogr.* 14, 912-920 (1969)
- and P.R. Sloan: Growth rates of marine phytoplankton: correlation with light absorption by cell chlorophyll a. *Physiologia Pl.* 19, 47-59 (1966)
- Frost, B.W.: Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* 17, 805-815 (1972)
- Garside, C., T.C. Malone, O.A. Roels and B.A. Sharfstein: An evaluation of sewage-derived nutrients and their influence on the Hudson Estuary and New York Bight. *Estuar. cstl mar. Sci.* 4, 281-289 (1976)
- Gaudy, R.: Feeding four species of pelagic copepods under experimental conditions. *Mar. Biol.* 25, 125-141 (1974)
- Goldman, J.C. and E.J. Carpenter: A kinetic approach to the effect of temperature on algal growth. *Limnol. Oceanogr.* 19, 756-766 (1974)
- and J.H. Ryther: Temperature-influenced species competition in mass cultures of marine phytoplankton. *Biotechnol. Bioengng* (In press)
- Guillard, R.R.L., P. Kilham, and T.A. Jackson: Kinetics of silicon-limited growth in the marine diatom *Thalassiosira pseudonana* Hasle and Heimdal (= *Cyclotella nana* Hustedt). *J. Phycol.* 9, 233-237 (1973)
- Jørgensen, E.G.: The adaptation of plankton algae II. Aspects of the temperature adaptation of *Skeletonema costatum*. *Physiologia Pl.* 21, 423-427 (1968)
- Laws, E.A.: The importance of respiration losses in controlling the size distribution of marine phytoplankton. *Ecology* 56, 419-426 (1975)
- Malone, T.C.: The relative importance of nanoplankton and netplankton as primary producers in the California Current System. *Fish. Bull. U.S.* 69, 799-820 (1971a)
- Diurnal rhythms in netplankton and nanoplankton assimilation ratios. *Mar. Biol.* 10, 285-289 (1971b)
- The relative importance of nanoplankton and netplankton as primary producers in tropical oceanic and neritic phytoplankton communities. *Limnol. Oceanogr.* 16, 633-639 (1971c)
- Phytoplankton productivity in the apex of the New York Bight: September 1973-August 1974. NOAA tech. Memo. U.S. Dep. Comm. ERL MESA-5 (1976)
- Phytoplankton productivity in the apex of the New York Bight: environmental regulation of productivity/chlorophyll a. In: *The middle Atlantic continental shelf and New York Bight*, Ed. by M. Grant Gross. *Limnol. Oceanogr.* (Special Symp. 2), (In press, a)
- Environmental regulation of phytoplankton productivity in the lower Hudson Estuary. *Estuar. cstl mar. Sci.* (In press, b)
- Mandelli, E.F., P.R. Burkholder, T.E. Doheny and R. Brody: Studies of primary productivity in coastal waters of southern Long Island, New York. *Mar. Biol.* 7, 153-160 (1970)
- Martin, J.H.: Phytoplankton-zooplankton relationships in Narragansett Bay. IV. The seasonal importance of grazing. *Limnol. Oceanogr.* 15, 413-418 (1970)
- McCarthy, J.J., W. Rowland Taylor and M.E. Loftus: Significance of nanoplankton in the Chesapeake Bay estuary and problems associated with the measurement of nanoplankton productivity. *Mar. Biol.* 24, 7-16 (1974)
- Mullin, M.M.: Some factors affecting the feeding of marine copepods of the genus *Calanus*. *Limnol. Oceanogr.* 8, 239-250 (1963)
- Munk, W.H. and G.A. Riley: Adsorption of nutrients by aquatic plants. *J. mar. Res.* 11, 215-240 (1952)
- Paasche, E.: On the relationship between primary production and standing stock of phytoplankton. *J. Cons. perm. int. Explor. Mer* 26, 33-48 (1960)
- Parsons, T.R. and M. Takahashi: Environmental control of phytoplankton cell size. *Limnol. Oceanogr.* 18, 511-515 (1973)
- Richman, S. and J.N. Rogers: The feeding of *Calanus helgolandicus* on synchronously growing populations of the marine diatom *Ditylum*

- brightwellii*. *Limnol. Oceanogr.* 14, 701-709 (1969)
- Ryther, J.H.: Photosynthesis and fish production in the sea. *Science, N.Y.* 166, 72-76 (1969)
- Saijo, Y. and K. Takesue: Further studies on the size distribution of photosynthesizing phytoplankton in the Indian Ocean. *J. oceanogr. Soc. Japan* 20, 264-271 (1965)
- Semina, H.J.: Water movements and the size of phytoplankton cells. *Sarsia* 34, 267-272 (1968)
- The size of phytoplankton cells in the Pacific Ocean. *Int. Revue ges. Hydrobiol.* 57, 177-205 (1972)
- Simpson, H.J., D.E. Hammond, B.L. Deck and S.C. Williams: Nutrient budgets in the Hudson River estuary. In: *Marine chemistry in the coastal environment*, Ed. by T.M. Church. *Symp. Ser. Am. chem. Soc.* 18, 618-635 (1975)
- Smayda, T.J.: A quantitative analysis of the phytoplankton of the Gulf of Panama. II. On the relationship between C<sup>14</sup> assimilation and the diatom standing crop. *Bull. inter-Am. trop. Tuna Commn* 9, 467-531 (1965)
- The suspension and sinking of phytoplankton in the sea. *Oceanogr. mar. Biol. A. Rev.* 8, 353-414 (1970)
- Stemann Nielsen, E. and E.A. Jensen: Primary oceanic production. The autotrophic production of organic matter in the ocean. *Galathea Rep.* 1, 49-136 (1957)
- Stommel, H.: Trajectories of small bodies sinking slowly through convection cells. *J. mar. Res.* 8, 24-29 (1949)
- Strickland, J.D.H. and T.R. Parsons: A practical handbook of seawater analysis. *Bull. Fish. Res. Bd Can.* 167, 1-311 (1972)
- Taguchi, S.: Relationship between photosynthesis and cell size of marine diatoms. *J. Phycol.* 12, 185-189 (1976)
- Takahashi, M., K. Fujii and T.R. Parsons: Simulation study of phytoplankton photosynthesis and growth in the Fraser River estuary. *Mar. Biol.* 19, 102-116 (1973)
- Teixeira, C.: Relative rates of photosynthesis and standing stock of net phytoplankton and nanoplankton. *Bolm Inst. Oceanogr., S Paulo* 13, 53-60 (1963)
- Thomas, W.H.: On nitrogen deficiency in tropical Pacific Ocean phytoplankton: photosynthetic parameters in poor and rich water. *Limnol. Oceanogr.* 15, 380-385 (1970)
- and A.N. Dodson: On nitrogen deficiency in tropical Pacific oceanic phytoplankton. II. Photosynthetic and cellular characteristics of a chemostat-grown diatom. *Limnol. Oceanogr.* 17, 515-523 (1972)
- Williams, R.B.: Division rates of salt marsh diatoms in relation to salinity and cell size. *Ecology* 45, 877-880 (1964)
- and M.B. Murdoch: Phytoplankton production and chlorophyll concentrations in the Beaufort Channel, North Carolina. *Limnol. Oceanogr.* 11, 73-82 (1966)
- Yentsch, C.S. and J.H. Ryther: Relative significance of the net phytoplankton and nanoplankton in the waters of Vineyard Sound. *J. Cons. perm. int. Explor. Mer* 24, 231-238 (1959)

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