Temporal enhancement
Nanoplankton
Netplankton
Production

Variation temporelle
Croissance
Nanoplancton
Microplancton
Production

Temporal variation of size-fractionated primary production in Bedford Basin during the spring bloom

D. V. SUBBA RAO [a], **S. J. SMITH** [b]

[a] Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada.

[b] Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada.

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ABSTRACT

During spring 1977, phytoplankton from Bedford Basin were subjected to standard size-fractionation procedures and variations in biomass and primary production were studied. The duration of the 1977 bloom was longer than those of 1974 and 1976, lasting 64 days with a wide range of biomass (1.46-18.8 µg Chl al^{-1}), production (3.51-63.7 mg C h^{-1} m^3) and carbon assimilation ratios (0.89-4.61 mg C h^{-1} mg Chl a^{-1}).

Nanoplankton (<20 µm fraction) contributed 8 to 64% of the biomass ($\bar{x}$=25%) and 8 to 56% ($\bar{x}$=23%) of the production and was usually low but varied over time.

Trends in phytoplankton biomass and primary production were compared with variables derived from Principal Component Analysis of chemical and physical variables measured over the same time. The trends in net plankton biomass and production appeared to be more related to the principal component scores derived from the chemical variables than were the trends of the nanoplankton. Neither fraction showed much relation with the scores from the physical variables although there was a significant positive correlation between nanoplankton biomass and productivity, and photosynthetically active radiation. Evidence was provided which indicated that selective grazing pressure on nanoplankton by zooplankton seemed to result in the dominance of the net phytoplankton.

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RÉSUMÉ

Variation temporelle de la production primaire suivant les classes de tailles dans le bassin de Bedford, pendant la floraison printanière

Au cours du printemps 1977, le phytoplancton du bassin de Bedford a été fractionné suivant des classes de tailles standard sur lesquelles les variations de la biomasse et de la production primaire ont été suivies. La durée de la floraison de 1977 a été plus longue que celles de 1974 et 1976, soit 64 jours, avec de grandes variations dans les valeurs de la biomasse (1,46-18,8 µg Chl a. l^{-1}), de la production (3,51-63,7 mg C.h^{-1}.m^{-3}) et des taux d'assimilation du carbone (0,89-4,61 mg C.h^{-1}.mg Chl a^{-1}).

Le nanoplancton (fraction < 20 µm) a contribué pour 8 à 64% ($\bar{x}$ 25%) de la biomasse et pour 8 à 56% ($\bar{x}$ 23%) de la production, en restant généralement faible mais variable dans le temps.

Les tendances pour la biomasse phytoplanctonique et la production primaire ont été comparées aux variables, dérivées de l'analyse du composant principal des variables chimiques et physiques mesurées pendant cette même période. Les tendances pour la biomasse phytoplanctonique globale et la production paraissent mieux reliées aux coordonnées du composant principal dérivées des variables chimiques, que ne le sont les tendances pour le nanoplancton. Aucune fraction n'a montré de bonnes relations avec les coordonnées correspondant aux variables physiques, bien qu'il y ait une corrélation positive significative entre la biomasse du nanoplancton, la productivité et

l'énergie radiative active dans la photosynthèse. On a montré que la pression sélective du broutage sur le nanoplancton semble plutôt résulter de celle sur le phytoplancton global.

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INTRODUCTION

In temperate coastal waters during spring a progression of events such as increased radiation, an increase in the depth of the euphotic layer and simultaneous development of some physical stability in the water column results in an increase of phytoplankton growth leading to a bloom (*see* Sinclair *et al.*, 1981), in which case production can be described as an amplitude and the duration as the time interval between initial and terminal phases (Cushing, 1975; Subba Rao, 1981). The duration of the spring bloom in temperate waters is usually 2 to 3 weeks (*see* Cushing, 1975) following which it becomes nutrient limited.

Herbivore grazing (Garrison, 1976), size-dependent differences in growth response to environmental conditions (Parsons, Takahashi, 1973; Malone, 1977) could result in varying degrees of dominance of either the nanoplankton (<20 µm) or the larger-celled netplankton, the two size-classes of phytoplankton (*see* Eppley, Weiler, 1979). Although there is sufficient evidence to support that the predominance of nanoplankton in temperate estuaries and coastal eutrophic waters is mainly due to excess grazing pressure upon netplankton (Garrison, 1976), information on excess grazing pressure on nanoplankton leading to dominance of netplankton is lacking (Eppley, Weiler, 1979).

Although the spring phytoplankton production in the coastal inlets of Nova Scotia was examined previously (Platt, Subba Rao, 1970; Platt, 1971) variations in biomass and photosynthetic production among different size-classes of phytoplankton have not been studied. The objectives of this study are to relate the temporal variations in the net and nanoplankton biomass and production of the spring phytoplankton bloom from an eutrophic temperate basin to the physical and nutrient data and to grazing by zooplankton. Requirements of phosphate and silicate by this bloom which is mostly dominated by diatoms were evaluated. Because of multicollinearity between the physico-chemical variables, Principal Component Analysis (PCA) was employed to analyse whether the variations in the net and nanoplankton were related to different principal components derived from the physico-chemical variables. The contribution of the nanoplankton either to the total biomass or total production and the role of selective grazing on nanoplankton in several temperate waters was also examined.

MATERIALS AND METHODS

Measurements of phytoplankton biomass and primary production were made on water samples collected twice a week from a fixed station located in Bedford Basin during the period 16 February through 4 May 1977. Using a Niskin water sampler, 46 l of water were collected from 5 m depth and stored in a carboy kept in a large fiberglass tank through which water from the Basin was circulated to simulate *in situ* temperature. The water sample was mixed well and a 6 l sample was drawn and used as an unfractionated (whole) sample.

From the remainder, a 6 l sample was passed through a Nitex sieve of 160 µm pore size and the filtrate designated the <160 µm fraction. Similarly, <100, <54, and <20 µm fractions were obtained and used for various measurements. Chlorophyll *a* was determined by the fluorometric method of Holm-Hansen *et al.*, 1965, using duplicate samples of 250 ml passed through Whatman GF/C (0.8 µm nominal porosity) filters treated with $MgCO_3$. Freshly collected samples and samples preserved with Lugol's iodine were examined under an inveted microscope. For carbon assimilation experiments (Steemann Nielsen, 1952) 100 ml samples were added to three light and one dark Pyrex bottle and a known activity of $NaH^{14}CO^3$ (5 µ Ci) was added after which each was stoppered and mixed. Samples were incubated for 4 h in a Perspex tank through which Bedford Basin water was circulated, illuminated by Sylvania 150 W projector flood lamps and fluorescent lights at a light energy of 300 µE m^{-2} s^{-1}. After incubation, samples were filtered through 0.45 µm HAWP Millipore filters and stored over silicagel. Filters were exposed to fuming HCl and counted following Subba Rao (1975). Methods for determination of the added activity of the bicarbonate, sample activity and calculation of primary production are described earlier (Subba Rao, 1975). Values from <20 µm fractions are considered as representative of nanoplankton, and are subtracted from those for unfractionated water to obtain "netplankton" values.

Hydrographical data were taken from the technical report No. 93 (Irwin, Platt, 1978). River discharge data are from Inland Waters Directorate (Anonymous, 1978). From the solar radiation data (Anonymous, 1977), photosynthetically active radiation (PAR 380-729 nm) was calculated following Sestak *et al.* (1971).

RESULTS

Increase in biomass was initiated during the second week of February, 1977. Phytoplankton biomass and production attained a peak during the second week of March and gradually decreased to almost the initial levels by early May (Fig. 1).

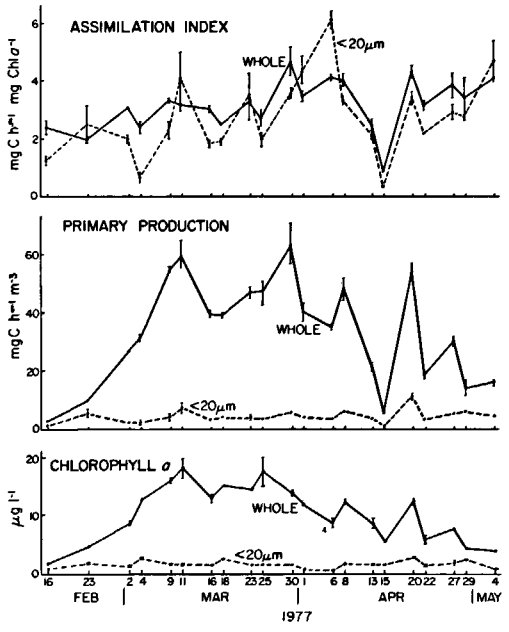


Figure 1

Variations in phytoplankton biomass and production of the unfractionated and nanoplankton (<20 µm) samples obtained from 5 m during spring 1977. Vertical bars indicate the 95% confidence limits.

Phytoplankton retained on the 160 µm mesh was not consistently high and on 8 out of 21 sampling dates it accounted for 1-19% ($\bar{x}=10$, S.D.$=6$) of the total biomass and 1-32% ($\bar{x}=8$, S.D.$=9.9$) of the total production. Both chlorophyll *a* and primary production levels in the various size fractions >20 µm were comparable and higher than those for nanoplankton (Tab. 1). The trend in the assimilation index, mg C h^{-1} mg Chl $a l^{-1}$ in size fractions >20 µm in general resembled that of production. The assimilation index ratios for the nanoplankton mostly ran parallel to those of other size fractions. However, on 6 out of 21 sampling days the nanoplankton had higher assimilation numbers than the rest of the fractions (Fig. 1).

Diatoms dominated the more than 35 species present. Present were centric forms *Biddulphia mobiliensis, B. pulchella, Chaetoceros affinis, C. atlanticum, C. coarctatum, C. compressum, C. debile, C. septentrionale, C. sociale, Coscinodiscus* sp., *Leptocylindrus* sp., *Rhizosolenia alata, R. setigera, Skeletonema costatum, Thalassiosira decipiense, T. hyalinum, T. nordenskioldii;* pennales such as *Fragilaria* sp., *Navicula* sp., *Gyrosigma* sp., *Nitzschia closterium, N. seriata, Nitzschia* sp., *Thalassionema nitzschioides, Thalassiothrix frauenfeldii;* dinoflagellates such as *Amphidinium* sp., *Dipsolapsis* sp., *Dinophysis norwegica, Gymnodinium* sp., *Gyrodinium* sp., *Peridinium depressum, P. oceanicum, Peridinium* sp., a number of microflagellates (<20 µm), the silicoflagellate *Distephanus speculum* and choanoflagellates. Of these the dominant species, *Chaetoceros affinis* ($<0.1\times10^6$ cells l^{-1}), *C. atlanticus* ($<0.002\times10^6$), *C. septentrionale* ($<4.4\times10^6$), *Nitzschia closterium* (0.45×10^6), *Skeletonema costatum* ($<1.8\times10^6$), *Thalassiosira decipiense* ($<0.13\times10^6$), *T. hyalinum* ($<0.13\times10^6$) and *T. nordenskioldii* ($<0.34\times10^6$) were present throughout the bloom and together contributed up to 60% of the cell numbers. The only minor changes were the presence of *Rhizosolenia* ($<0.3\times10^6$) from 11 March onwards in considerable numbers and the replacement of *C. affinis* in early April by *C. debile* which flourished until 4 May. Except for these changes, the composition of the bloom was maintained. Although the microflagellates did not dominate the phytoplankton biomass, they were abundant on 23 February, 2, 11, 25 March, 1, 6, 29 April and 4 May.

DISCUSSION

The longer than usual duration of the 1977 spring bloom was a feature of interest. Earlier results from Bedford Basin showed that in 1970 the spring bloom was of 4 weeks duration (Platt, Irwin, 1971), 3 weeks in 1971 (Platt *et al.*, 1973) and 4 weeks in 1974 (Taguchi *et al.*, 1975). In 1976, the duration was 7 weeks with peak values of biomass of 22.92 µg Chl *a* l^{-1}, and production of 73.57 mg C h^{-1} m^{-3} with corresponding amplitudes of 23.39 and 20.91 (Tab. 2). In 1977 the duration of the bloom was 9 weeks and thus even longer than in the previous year. Biomass ranged between 1.46 and 18.83 µg Chl *a* l^{-1} and production from 3.51 to 63.66 mg C h^{-1} m^{-3} and the amplitudes were 12.90 and 18.14 respectively (Tab. 2).

Studies in other temperate coastal waters show enhancement of phytoplankton blooms for more than 3 weeks, similar to those in the present study; included are those from New York Bay (O'Reilly *et al.*, 1976), Narragansett Bay (Durbin *et al.*, 1975), Chesapeake Bay (Loftus *et al.*, 1972), Trondheimsfjord (Sakshaug and Myklestad, 1973) and Dutch coastal waters (Gieskes, Kraay, 1975) although only the last two deal with spring bloom. There are some contrasting features between the blooms that occurred in Chesapeake Bay

Table 1

Chlorophyll a, *primary production and assimilation index values in the various fractions during spring bloom* 1977 ($n=21$).

Fraction	Chl *a* µg l^{-1}			Primary production mg C h^{-1} m^{-3}			Assimilation index mg C h^{-1} mg Chl a^{-1}		
	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.
Whole	1.46-18.8	10.29	4.95	3.51-63.7	33.26	18.18	1.99-4.61	3.51	0.88
<160 µm	1.55-19.3	10.41	5.43	3.86-62.2	33.53	18.50	1.04-4.90	3.23	0.95
<100	1.60-1.80	9.24	4.81	4.00-57.9	30.32	16.91	0.89-4.76	3.28	1.00
<54	1.47-15.4	7.04	3.95	3.88-42.8	20.87	11.72	0.91-4.60	3.01	0.91
<20	0.43-2.99	1.58	0.61	1.20-10.3	4.06	2.08	0.40-6.04	2.79	1.32

Table 2

Duration, range and amplitude of spring phytoplankton blooms in Bedford Basin.

Year	from	to	Days	Number obser.	Range			Amplitude			References
					Chl *a* $\mu g\ l^{-1}$	Primary production mg C h^{-1} m^3	Assimilation index mg C h^{-1} mg Chl *a*	Chl *a*	Primary production	Assimilation index	
1974	March 6	April 3	28	5	0.88-10.65	3.75- 9.81	0.51-11.19	3.56	2.60	11.8	Taguchi *et al.*, 1975(1)
1976	February 17	April 9	51	16	0.98-22.92	3.52-73.57	2.57-3.55	23.39	20.91	1.26	Irwin, Platt, 1978(2)
1977	February 16	May 4	64	21	1.46-18.83	3.51-63.66	0.89-4.61	12.90	18.14	5.18	Present study(2)

(1) *In situ* incubations; chlorophyll data based on 10 observations.
(2) Incubators were illuminated by a 150 W flood light.

and the Dutch coastal waters. The duration of the bloom in Chesapeake Bay was 3 weeks, during August in response to a pulse in freshwater runoff, the amplitude of biomass was 40X and nanoflagellates (<20 µm) were dominant. In the Dutch waters the bloom lasted for 10 weeks, dominated by chain diatoms as in Bedford Basin. However, the run off from the Rhine, although causing nutrient enrichment, also increased the turbidity; as a consequence the amplitude of biomass and production in the Dutch waters was lower than that from Bedford Basin. In Trondheimsfjord, following winter accumulation of nutrients, the spring bloom initiated and ran its course in about 4 weeks. According to Sakshaug and Myklestad (1973) this phase is analogous to a "batch culture". But then with replenishment of nutrients contributed by unusually high run off, the spring bloom had an extended duration similar to that which was observed in Bedford Basin, a phase which Sakshaug and Myklestad (1973) regarded as a "continuous culture" analog.

The dissolved N:P atomic ratios in the initial stages of the bloom were higher (9-10) and decreased to low (0.8-3.7) towards the end of the bloom. Physical and nutrient data show (Fig. 2) that in the initial stages of the bloom the levels of all nutrients were high for about 3 weeks, and decreased until about 16 March. By then both the biomass and primary production had attained peak values and the bloom under normal conditions should have begun to diminish because of depleted nutrients, but this was not the case. The pulse in river flow in early April may have increased the flux of new nutrients, possibly phosphate and silicate, and thus the timing of the spring run-off peak could have an effect on the amplitude and duration of the spring bloom.

Phosphate in excess of the demand by phytoplankton in the water was calculated following the method of Ryther and Dunstan (1971) who assumed that all nitrogen was assimilated as produced and that phosphorus was assimilated at a nitrogen to phosphorus atomic ratio of 10:1 ($=4.522$:1 on weight-basis) in the eutrophic coastal waters off Long Island.

During 1977 the duration, range and amplitude of the phytoplankton bloom were higher than in 1974 and 1976 (Tab. 2). For 1976, the duration was 51 days with a biomass range of 0.98 to 22.92 µg Chl *a* l^{-1}, and production of 3.52 to 73.57 mg C h^{-1} m^{-3} with corresponding amplitudes of 23.39 and 20.91 (Tab. 2). For 1977 the duration of the bloom was 64 days and thus even longer than the earlier years. Biomass ranged between 1.46 and 18.83 µg Chl *a* l^{-1} and production from 3.51 to 63.66 mg C h^{-1} m^{-3} and the amplitudes were 12.90 and 18.14 respectively (Tab. 2).

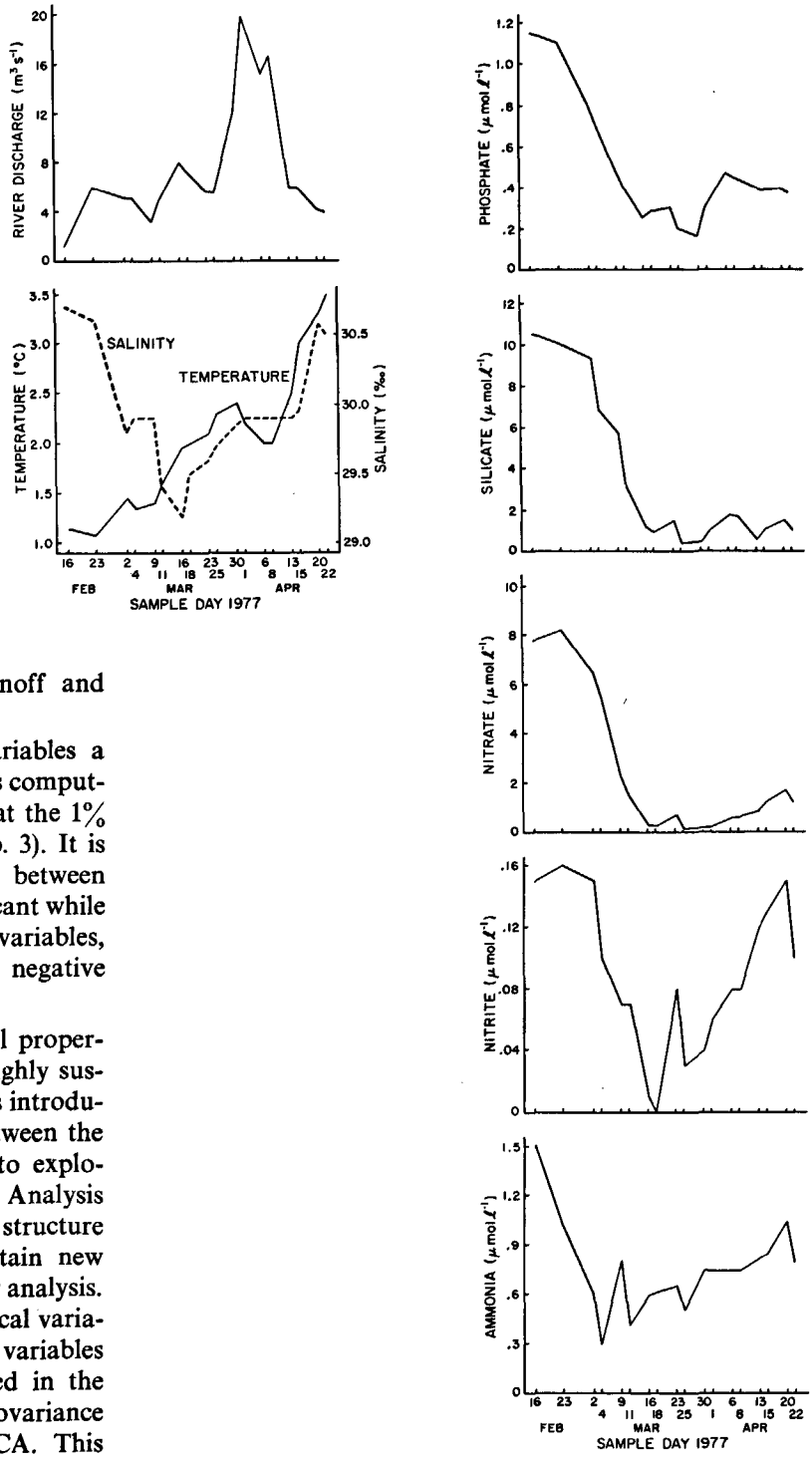
Due to sufficiency of phosphate throughout the season, indicated by excess phosphate which ranged between 0.05 and 0.27 µg at l^{-1} with high values (0.14 to 0.27) from the third week of March, there was a sustained growth of phytoplankton. It must be pointed out that at the onset of the bloom the total nitrogen and phosphate ratios were high (9 to 10) and steadily decreased as the bloom lasted (Fig. 2). The rapid utilization of nitrogen or rapid recycling of phosphate must have resulted in the lower N:P ratios. However, to assess the role of nutrients in river runoff, the actual input of nutrients by the river, vertical stability of the column, exchanges between the basin and coastal waters, standing stocks of nutrients in the basin and utilization rates by the phytoplankton should be considered and the data needed for this approach are not available.

As this bloom is mostly dominated by diatoms that require silicon for frustule formation, it could be silicate limited. Silicate was plotted against net phytoplankton particulate nitrogen (PN) which was coincidentally determined for this spring bloom (Irwin, Platt, 1978). There was a sharp break between the netplankton nitrogen and silicate at a silicate concentration of 1.1 µg at l^{-1} which is similar to that observed by Malone *et al.* (1980). The regression equation is:

$Si = 9.803 - 0.055$ (PN); $r^2 = 0.749$, $F = 17.9$, 7 d.f., $P < 0.01$).

This relationship, however, was not significant when the silicate levels less than 1.1 µg at l^{-1} were included, that is from March 16, excepting 22 March, 5 and 20 April when it was about 1.5 µg at l^{-1} (Fig. 2). The netplankton biomass and production during this period however, continued to be high which suggests that the silicate requirements were being met. Possibly high runoff from Sackville river on 11, 16 March, 1, 2, and 27 April, supplemented the supply of this nutrient. The data are insufficient to establish with certainty lags between river runoff, nutrient enrichment and appearance of netplankton blooms, but there seems to

Figure 2
Variations in river discharge, temperature, salinity and nutrients during spring 1977.



be a time lag of 4-7 days between the runoff and phytoplankton peak.

From our data on the physico-chemical variables a 10 x 10 matrix of correlations (parametric) was computed. Of these correlations 20 were significant at the 1% probability level and 4 at the 10% level (Tab. 3). It is of interest to note that the correlations between nutrients and salinity were positive and significant while those between the nutrients and the physical variables, *i.e.* daylength, runoff and temperature were negative and significant.

Use of regression analysis to relate biological properties, *i.e.* biomass and production would be highly suspect here due to the multicollinearity problems introduced by the high levels of intercorrelations between the physico-chemical variables. Therefore prior to exploring such relationships Principal Component Analysis (PCA) was used to analyze the correlation structure between these variables and in turn to obtain new uncorrelated (orthogonal) variables for further analysis. It was decided to treat the physical and chemical variables separately for our analysis. The chemical variables with the exception of salinity were measured in the same units which allows one to use the covariance matrix and the raw observations in the PCA. This

Table 3

Summary of coefficients of correlation between physical variables.

Variable	Day length	PAR	Run off	Temp.	S	PO_4	SiO_2	NO_3	NO_2	NH_3
Day length	–	–	–	–	–	–	–	–	–	–
PAR	0.45*	–	–	–	–	–	–	–	–	–
Run off	–	–	–	–	–	–	–	–	–	–
Temp.	0.90**	–	–	–	–	–	–	–	–	–
S	–	–	–	–	–	–	–	–	–	–
PO_4	−0.68**	–	–	−0.63**	0.60**	–	–	–	–	–
SiO_2	−0.81**	–	−0.42*	−0.74**	0.44*	0.94**	–	–	–	–
NO_3	−0.74**	–	−0.45*	−0.63**	0.55**	0.96**	0.97**	–	–	–
NO_2	–		—	–	0.75**	0.72**	0.60**	0.70**	–	—
NH_3	–	–	–	−0.60**	0.77**	0.51**	–	–	0.55**	–

1, 16 d.f. * Exceeds value expected at 10% probability level but less than 1%.
** Exceeds value expected at 1% probability level.

Table 4

Summary of Principal Component Analysis of chemical variables showing the components, percentage variance and component coefficients.

Component	Percentage variance explained	Coefficients				
		PO_4	SiO_2	NO_3	NO_2	NH_3
1	98.2	0.061	0.798	0.609	$7.073E^{-3}$	0.022
2	1.36	0.068	−0.610	0.777	0.041	0.130
3	0.29					
4	0.02					

has certain statistical appeal in that the ith principal component can be interpreted as explaining the ith largest proportion of the total response variance of the actual data (Morrison, 1976, p. 268). Whereas use of the correlation matrix which was the case for the physical variables due to the many different scales of measurement refers to a standardisation of the original data.

The PCA on the chemical variables (Tab. 4) showed that 98.32% of the total variance was accounted for by the first principal component (PC1). Salinity was removed from the final analysis because it varied little over the study period. The first component was essentially a weighted sum of nutrient concentrations with silicate and nitrate receiving the largest weights (Tab. 4). A comparison of trends over time between PC1 and silicate and nitrate is given in Figure 3. The first component scores closely follow the trends of these two nutrients with high values initially, followed by an almost exponential decrease to oscillate around low concentrations for the remainder of the time.

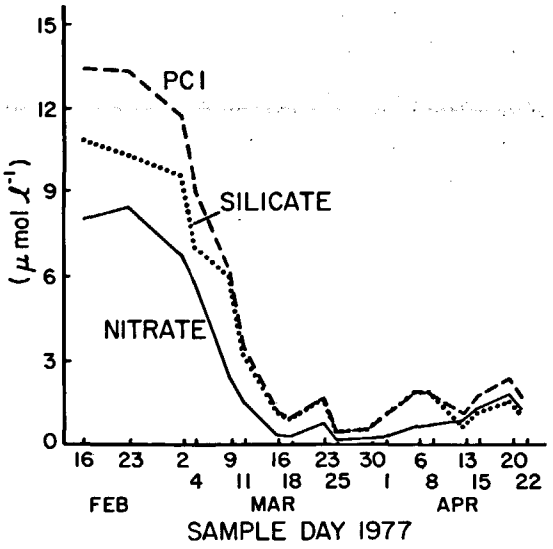


Figure 3
Comparison of PC1 (nutrient) with silicate and nitrate concentrations.

The situation for the physical variables was more complex with the first three components being required to explain as much as the first component in the case above. The first component given in Table 5 is a weighted sum with runoff given the smallest weight. In the second component daylength and runoff is contrasted with photosynthetic available radiation.

The next step in the analysis was to compare the biological properties with the newly derived variables from the PCA specifically the PC1's for the physical and nutrient (chemical) variables. In Figure 4*a* and 4*b*

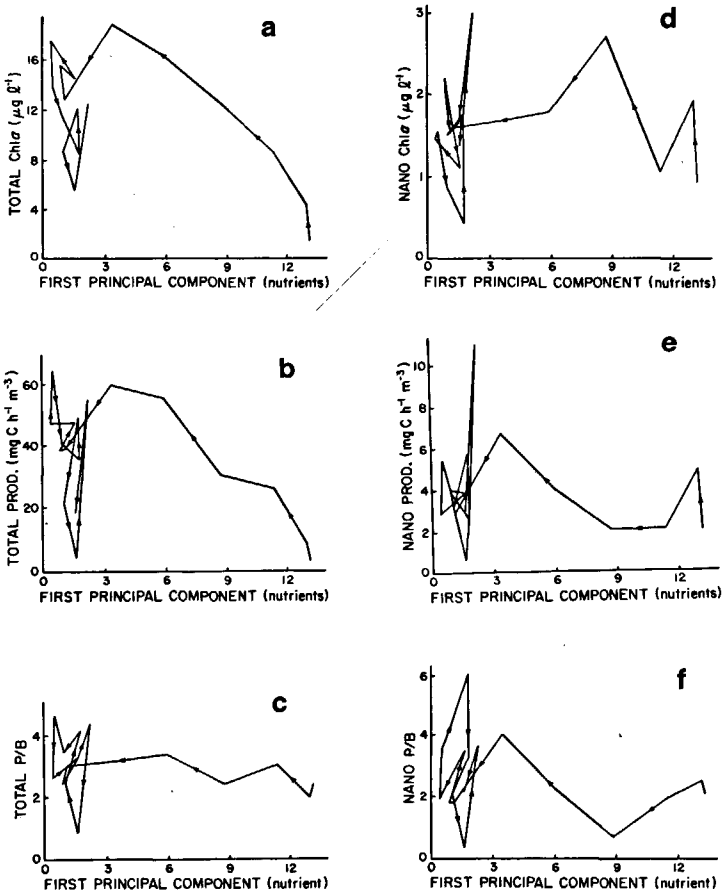


Figure 4
a) *Total chlorophyll* a vs 1*st PC score (nutrients, covariance matrix). Arrows indicate temporal progression.*
b) *Total production* vs 1*st PC score (nutrients, covariance matrix). Arrows indicate temporal progression.*
c) *Total P/B* vs 1*st PC score (nutrients, covariance matrix). Arrows indicate temporal progression.*
d) *Nano production* vs 1*st PC score (nutrients, covariance matrix). Arrows indicate temporal progression.*
e) *Nano chlorophyll* a vs 1*st PC score (nutrients, covariance matrix). Arrows indicate temporal progression.*
f) *Nano P/B* vs 1*st PC score (nutrients, covariance matrix). Arrows indicate temporal progression.*

Table 5

Summary of Principal Component Analysis of physical variables showing the components, percentage variance and component coefficients.

Component	Percentage variance explained	Coefficients			
		Daylength	PAR	Run off	Temperature
1	55.65	0.649	0.414	0.138	0.623
2	30.45	0.165	−0.537	0.827	$2.212\ E^{-3}$
3	12.81				
4	1.08				

total chlorophyll *a* and primary production were plotted against PC1 (nutrient). Two phases appear to be discernable with the first occurring during the first 6 samples (till March 11th) where biomass and production increased concurrent with a decrease in nutrient concentrations (specifically silicate and nitrate). In the second phase which appears to encompass the remaining samples, nutrient levels remained low while biomass and production decreased with this decrease being more pronounced for biomass.

Trends for nanoplankton biomass and production differed from that for the total (Fig. 4*d* and 4*e*). The nanoplankton did not exhibit a rapid and sustained increase as was the case for the total during the first 6 sampling dates. Oscillations also appeared to be more pronounced for the nanoplankton during the last 12 sample dates.

Comparison of biomass and production with PC1 (physical variables) proved less than informative. Generally the physical variables increased in value over time with occasional surges in runoff. The patterns for total and nanoplankton biomass with respect to PCl presented in Figure 5*a* and *b* respectively are definitely different but offer little in explanatory value. Use of Spearman rank correlation (Conover, 1971) to investigate possible relationships between PAR and the biomass and primary production for total and nanoplankton showed that there was no significant correlation for the total fraction. However nanoplankton biomass was positively correlated at the 5% level and primary production at the 10% level.

The trends for assimilation ratios (P/B) followed that of the biomass and production with nutrients (PCl)

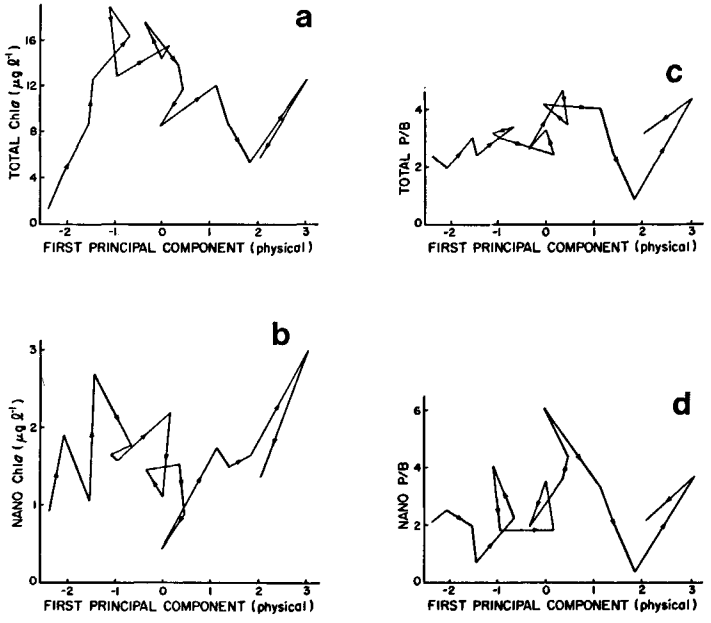


Figure 5

a) *Total chlorophyll* a vs 1*st PC score* (*physical, correlation matrix*). *Arrows indicate temporal progression.*
b) *Nano chlorophyll* a vs 1*st PC score* (*physical, correlation matrix*). *Arrows indicate temporal progression.*
c) *Total P/B* vs 1*st PC score* (*physical, correlation matrix*). *Arrows indicate temporal progression.*
d) *Nano P/B* vs 1*st PC score* (*physical, correlation matrix*). *Arrows indicate temporal progression.*

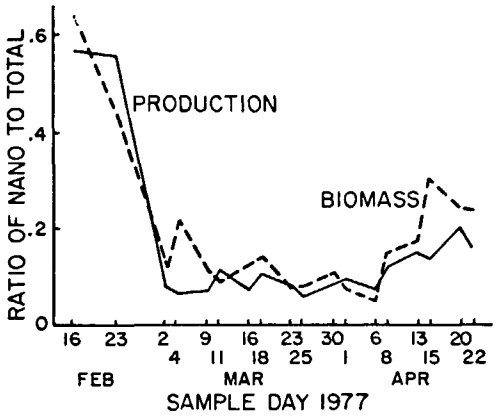


Figure 6

Ratio of nano: total (*biomass and production*).

i.e. the P/B for the total and nanoplankton generally increased during the first 6 samples with a decrease in nutrients, in the rest of the samples they oscillated while nutrient levels remained low (Fig. 4*c; f*). Comparison of P/B with physical variables (PCl) showed that as the physical variables progressively increased P/B also increased particularly for total phytoplankton but not for nanoplankton (Fig. 5*c; d*). The assimilation ratios for the total were significantly correlated ($r=0.752$, $p=0.002$) with those for the nanoplankton.

Thus the preceding analysis suggests that the different size fractions of the phytoplankton differ in their relationships to the variables studied here with the inference that the nutrient variables are more important for the net plankton while PAR appears to be more important for the smaller nanoplankton.

The contribution of the nanoplankton either to the total biomass or total primary production was not constant but varied over time. The ratios for nano to total biomass and production (Fig. 6) were initially high, decreased to a low but stable level and then showed an increase towards the end of the study. Comparison of the total and nano biomass and production by Spearman rank correlation indicated that trends in biomass were not correlated but that primary production was (Tab. 6).

Accepting 20 μm as the upper size limit of the nanoplankton a similar analysis was carried out on biomass and primary production data from selected studies of temperate waters in the literature (Tab. 6). With respect to biomass, only Narragansett (Durbin *et al.*, 1975) and Chesapeake Bay (Valkenberg, Flemer, 1974) showed a significant correlation between total and nanoplankton at the 5% level.

For all the areas investigated with the exception of Monterrey Bay (Garrison, 1976) primary production for the total and the nanoplankton fraction were significantly correlated at the 5% level. Note that for the areas listed in Table 6 the Monterey stations were located offshore and deeper than in the other studies. Garrison (1976) hypothesized that selective nanoplankton removal was being effected by either horizontal advection or by selectives grazing which may explain why this area was the exception to the trends in the other studies.

Table 6

Comparison of Spearman Rank correlations between the nano to total biomass and primary production in temperature waters.

Region	Depth m	Season	Biomass		Primary production		
			$\hat{\rho}$	P level	$\hat{\rho}$	P level	
New York Bight	<30	April-November	–	–	0.708	1.5×10^{-3}	Malone, 1977
Narragansett Bay	<9	February-March	0.635	4.51×10^{-4}	0.574	0.012	Durbin *et al.*, 1975
Lower New York Bay	14	Annual	–	–	0.944	1.74×10^{-3}	O'Reilly *et al.*, 1976
Peconic Bay	9	Annual	–	–	0.954	1.24×10^{-5}	Bruno *et al.*, 1983
Chesapeake Bay	66	Annual	0.553	0.067	–	–	McCarthy *et al.*, 1974
Chesapeake Bay	31	Annual	0.612	1.48×10^{-3}	0.507	0.020	Valkenburg and Flemer, 1974
Monterey Bay	110-728	Annual	−0.126	0.554	0.404	0.087	Garrison, 1976
Paramalta estuary	<22	June	–	–	0.955	2.16×10^{-4}	Relevante and Gilmartin, 1978
Bedford Basin	25	February-May	0.323	0.183	0.690	4.419×10^{-3}	Present study

Selective feeding on nanoplankton by zooplankton might contribute to the dominance of netphytoplankton during spring blooms. The utilization of phytoplankton by zooplankton during the bloom in the spring of 1977 was studied by Conover and Mayzaud (1984). The proportion of nanoplankton (<20.2 μm) ingested by zooplankton was calculated from their Coulter Counter data kindly supplied by Dr. R.J. Conover; some detritus will be included in this fraction. Comparison between netplankton production (Fig. 1) and total zooplankton ingestion (Fig. 7) during February and March when most of the grazing experiments were done shows that the netplankton production increased during periods of increased grazing by zooplankton (February 8-March 11, March 17-25). During these periods, of the total ingested, 40-69% ($\bar{x}=58\%$) was nanoplankton. Such selective predation could reduce and then maintain the low contribution by nanoplankton to the total phytoplankton, while lack of grazing pressure on net phytoplankton would account for its dominance. Our results compare favourably with the findings from other temperate coastal waters. Recall Garrison's (1976) suggestion that besides selective removal of nanoplankton by horizontal advection, selective grazing pressure by microzooplankton decreased nanoplankton in Monterey Bay. While nanoplankton blooms were limited by grazing in New York Bight, low grazing pressure on netplankton resulted in blooms of netplankton diatoms (Malone, Chevrin, 1979). The ecological significance of such selective grazing by herbivores on either nano or netplankton would be the dominance of the ungrazed fraction and conceivably shifts in the production efficiencies.

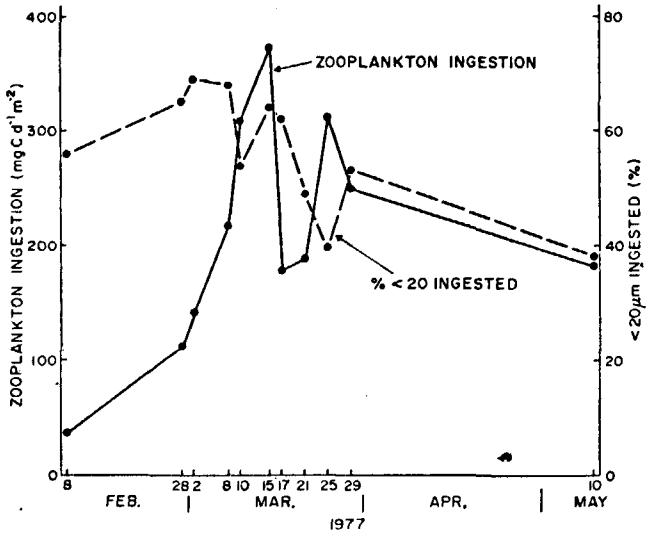


Figure 7
Zooplankton ingestion and the relative proportion (%) of nanoplankton ingested.

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