

The size distribution of phytoplankton and particulate organic matter in the Equatorial Atlantic Ocean: importance of ultrasteston and consequences

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Abstract. The size fractionation of particulate matter (<200 , <35 , <3 and $<1 \mu\text{m}$) has been measured in the Equatorial Atlantic Ocean at different stations. Chlorophyll *a*, phaeophytin, particulate carbon, nitrogen and phosphorus have been analysed. Primary production by $^{14}\text{CO}_2$ uptake was also measured with prescreening technique.

It appears from this study, that the particulate matter has a very small size: 40-60% of the chlorophyll passed through $1 \mu\text{m}$ Nucleopore filter, and 75-90% of the particulate carbon and nitrogen passed through $3 \mu\text{m}$ Nucleopore filter in offshore waters.

From the atomic ratio C/N, C/P and C/chla, and primary production values, the $<3 \mu\text{m}$ fraction would be mainly constituted by inactive photosynthetic organisms or particles of detritus. The 3-35 μm fraction, in contrast, would be principally active phytoplankton.

Introduction

As Malone *et al.* said in a recent note (1979) "Phytoplankton size classes have received much attention recently because of proposed influences of particulate size (cells and chains) on the population dynamics of phytoplankton (Williams, 1964; Eppley and Sloan, 1966; Malone, 1971 *a*) and energy flow through food chains (Ryther, 1969; Parsons and Lebrasseur, 1970; Walsh, 1976)".

Most of the studies on geographic variations in netplankton (>20 - $35 \mu\text{m}$) and nanoplankton (<20 - $35 \mu\text{m}$) primary productivity and standing crop have demonstrated that nanoplankton is often responsible for 80-99% of the observed phytoplankton productivity in both temperate (Yentsch and Ryther, 1959; Gilmartin, 1964; Anderson, 1965; Durbin *et al.*, 1975; Malone, 1977; McCarthy *et al.*, 1974) and tropical waters (Steemann-Nielsen and Jensen, 1957; Holmes, 1958; Teixeira, 1963; Ibarra, 1978). A common result is that nanoplankters were the most impor-

index of particle size of suspended material in the Eastern Tropical Pacific, concluded that the surface layer down to 40 m contains particles between 1 and 2 μm in diameter, whereas the particles below 400 m were relatively fine with diameters less than 0.4 μm .

In this study, the natural phytoplankton and particle population in the Equatorial Atlantic Ocean were fractionated into three or four size classes and the chlorophyll *a*, phaeophytin *a*, rates of carbon assimilation, particulate carbon, nitrogen and phosphorus were determined for each size class. Some methodological and ecological consequences are mentioned in the second part of the paper.

This study is a part of CIPREA, (Circulation et Production à l'Equateur dans l'Atlantique) a French multidisciplinary study program, supported by ORSTOM in the Equatorial Atlantic (1978-1980).

Material and methods

The results were obtained during three cruises of the RV Capricorne in the Gulf of Guinea in 1979 (Figure 1): SOP 1, a 14 day study at the Equator (0° - 4° W from 5 to 19 February), CIPREA II, a leg from Abidjan to Ste Helena Island (2 to 29 April) and CIPREA III, a survey cruise between 1° N and 5° S from 4° W to 6° E in the Gulf of Guinea. Temperature was recorded *in situ* with a Bisset Berman STD probe coupled with a Hewlett Packard computer. Sampling levels were chosen in terms of the temperature profiles in order not to miss the expected nutrient gradients and chlorophyll maxima. Samples from discrete depths were collected with PVC bottles of two capacities: 12 small bottles of 1.7 l from a "rosette sampler" (General Oceanic) to determine as well as possible the chlorophyll maximum layer and a 30 l Niskin bottle to collect the samples for particulate matter

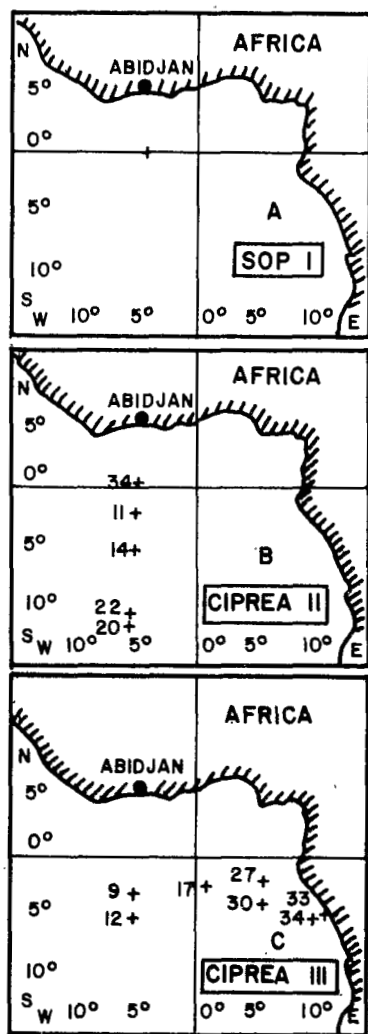


Fig. 1. Location of stations used in the study

sea water were filtered through 200, 35, 3 and/or 1 μm ; 300 ml BOD all-glass bottles were used for incubation in a deck incubator (simulated *in situ* condition at surface temperature); 4 μCi of $^{14}\text{CO}_2$ was added in each flask. After 5 h of incubation, the 300 ml were filtered through a Whatman GFC filter and rinsed with 10 ml of filtered sea water. The filters after drying at 55-60°C in the scintillation vials were counted for their radioactivity by liquid scintillation counter at the laboratory.

Results and Discussion

Size distribution of chlorophyll and particulate organic matter of the chlorophyll maximum layer in the Equatorial Atlantic at 4°W.

The mean profiles ($n = 14$) of temperature, nitrate, chlorophyll and primary production are shown in Figure 2. There is a warm mixed layer of 20-25 m ($t \cong 29^\circ\text{C}$) with quasi-undetectable nitrate and low values of chlorophyll a ($= 0.10 \mu\text{g l}^{-1}$). The thermocline is well developed. Chlorophyll a and primary production maxima are located above the nitrate gradient (= nitracline). Relative high

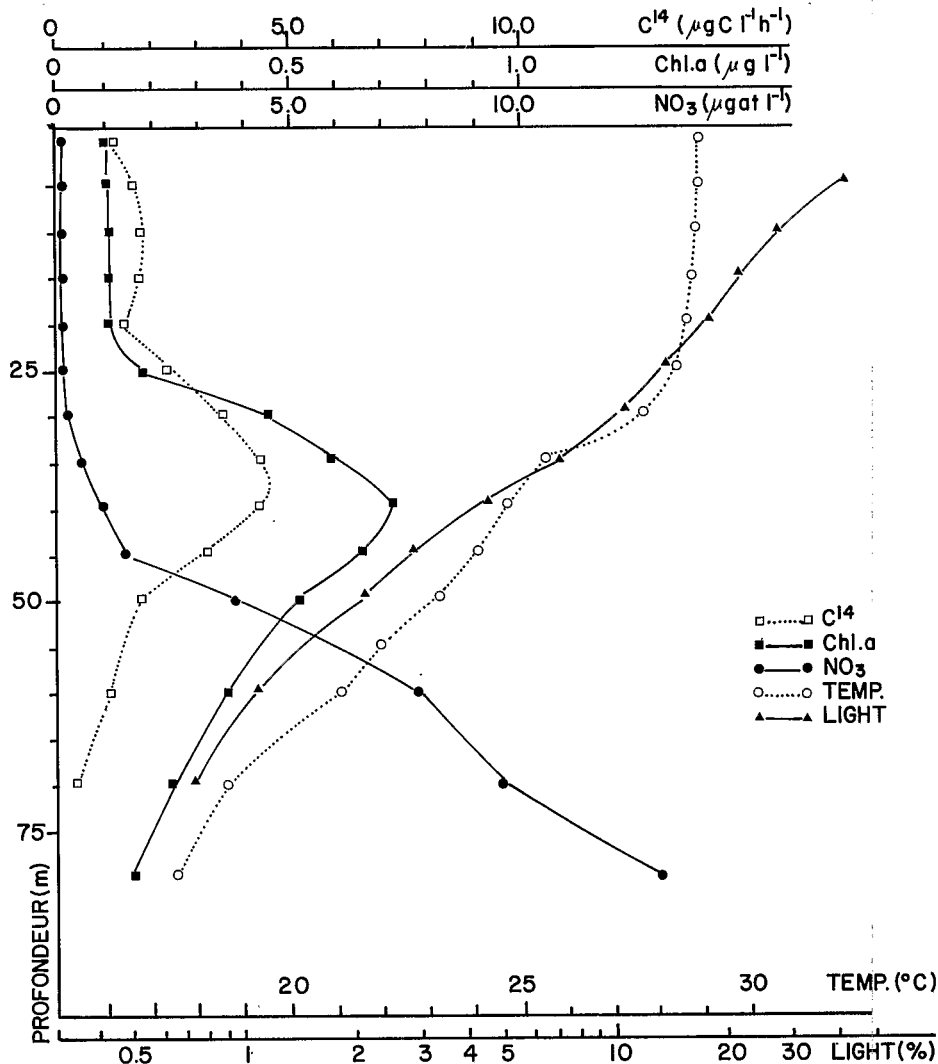


Fig. 2. The mean profiles of temperature, light, nitrate, chlorophyll a and $^{14}\text{CO}_2$ uptake during a long duration station (14 days) in the Equatorial Atlantic Ocean (0° - 4° W). Cruise SOP 1.

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values of chlorophyll ($\cong 1 \mu\text{g l}^{-1}$) and primary production ($5-7 \mu\text{gC l}^{-1} \text{h}^{-1}$) were observed. The 1% light level, which usually defines (but not truly) the bottom of the euphotic layer is near the depth of 60-65 m. It is the Typical Tropical Structures (TTS) as defined by Herbland and Voituriez (1979). During the first week of the station, the size distribution of chlorophyll *a*, phaeophytin *a* and primary production were measured on the same samples. The results are presented in Table I.

Chlorophyll and phaeophytin have a similar size distribution since 72% and 75% (mean values) respectively pass through $35 \mu\text{m}$ and 43% and 41% (mean values) through $3 \mu\text{m}$. The proportion of chlorophyll in particles smaller than $3 \mu\text{m}$ is surprisingly high. The phaeophytin rate ($[\text{phaeophytin}/(\text{phaeophytin} + \text{chlorophyll } a)] \times 100$) does not differ in the different size classes (range = 31-34%).

The size distribution of primary producers differs from the size distribution of chlorophyll containing particles: 88% of the total primary production is performed by the $35 \mu\text{m}$ filtered water and only 20% by the $3 \mu\text{m}$ filtered water. It would mean that a high percentage of the photosynthetic activity originates from

Table I. Size distribution of chlorophyll *a*, phaeophytin, primary production and assimilation number in the chlorophyll maximum layer of the Equatorial Atlantic Ocean (0°-4°W). Cruise SOP 1, February 1979. A 14-day study with one station per day.

St	chlorophyll <i>a</i>						phaeophytin <i>a</i>						¹⁴ Carbon uptake						Ass Number			Phaeophytin rate		
	$\mu\text{g l}^{-1}$			%			$\mu\text{g l}^{-1}$			%			$\mu\text{gC l}^{-1} \text{h}^{-1}$			%			$\mu\text{gC } \mu\text{gchl}a \text{ h}^{-1}$			%		
	<200	<35	<3	<200	<35	<3	<200	<35	<3	<200	<35	<3	<200	<35	<3	<200	<35	<3	<200	<35	<3	<200	<35	<3
2	0.85	0.57	0.37	100	67	44	0.47	0.28	0.16	100	60	34	-	-	-	-	-	-	35.6	32.9	30.2			
3	1.16	0.79	0.46	100	68	40	0.49	0.37	0.17	100	76	35	5.93	4.16	0.77	100	70	13	5.1	5.3	1.7	29.7	31.9	27.0
4	1.38	0.97	0.47	100	70	34	0.69	0.50	0.22	100	73	32	6.58	6.04	0.64	100	92	10	4.8	6.2	1.4	33.3	34.0	31.9
5	1.14	0.87	0.55	100	77	48	0.57	0.46	0.24	100	81	43	5.73	5.34	1.18	100	93	21	5.0	6.1	2.1	33.3	34.6	30.4
6	1.08	0.83	0.53	100	77	49	0.53	0.45	0.32	100	85	60	5.12	5.0	1.72	100	98	34	4.7	6.0	3.2	32.9	35.2	37.6
m	1.12	0.81	0.48	100	72	43	0.55	0.41	0.22	100	75	41	5.84	5.14	1.08	100	88	19.5	4.9	5.9	2.1	33.0	33.7	31.4
σ	0.19	0.15	0.07	0	4.9	6.2	0.09	0.09	0.06	0	9.6	11.5	0.60	0.78	0.49	0	12	11	0.18	0.41	0.8	2.1	1.3	3.9
Cv(%)	16.9	18.4	14.8	0	6.8	14.3	15.9	21.3	28.9	0	12.8	28.2	10.3	15.2	45.1	0	14	55	3.7	6.9	37.5	6.4	3.9	12.5

Table II. Mean calculated values for the 3-35 μm size class in the chlorophyll maximum layer of the Equatorial Atlantic Ocean ($0^\circ - 4^\circ\text{W}$). Cruise SOP 1, February, 1979.

	chlorophyll <i>a</i> $\mu\text{g l}^{-1}$	phaeophytin <i>a</i> $\mu\text{g l}^{-1}$	^{14}C uptake $\mu\text{gC l}^{-1}\text{h}^{-1}$	A.N. $\mu\text{gC } \mu\text{gchl}^{-1}\text{h}^{-1}$	phaeo. rate %
Value	0.36	0.19	4.09	11.2	36.5
% of < 200 μm	29.5	34.5	69.5	-	-

the values of healthy phytoplankton culture (Antia *et al.* 1963, McAllister *et al.*, 1961). Zeitzschel (1970) found an average phytoplankton carbon/chlorophyll ratio of 37.8 for mixed natural phytoplankton populations (our mean value is 34.4). With the high (but not accurate) assimilation numbers found in the week before, the 3-35 μm size class in these waters comprises phytoplankton cells with a low percentage of detritus.

Size distribution of chlorophyll particles in the Gulf of Guinea

In order to investigate the lower limit of the size distribution, other measurements, including 1 μm filtration, have been made during CIPREA II, in similar hydrological conditions (Typical Tropical Structure). Only chlorophyll *a* and phaeophytin *a* values are available (and particulate phosphorus at stations 11 and 14). The results are presented in Table V. They confirm the extreme smallness of particulate matter containing chlorophyll since 60% ($\sigma = 9.5$) of the chlorophyll passed through the 1 μm Nucleopore filter in the mixed layer waters (0 and 5 m) and 57.5% ($\sigma = 2.7$) in the thermocline layer. The particulate phosphorus has a similar distribution: respectively 47 and 41.3% of the phosphorus passed through 1 μm . A more unexpected result is found with the phaeophytin size distribution: in the mixed layer 96% of the phaeophytin passed through 1 μm and only 55% in the thermocline.

However, these high phaeophytin percentages could be the result of an artefact of methodology, when the values are very low. Chl *a* and phaeophytin were measured by a reading before and after acidification of the extract containing the glass fibre filter. If the blank values of Whatman filter are negligible for chl *a*, values between 0.005 $\mu\text{g l}^{-1}$ and 0.01 are commonly found for phaeophytin. If they are not subtracted to the sample values, the phaeophytin will be over-

Table III. Size distribution of particulate organic matter in the chlorophyll maximum layer of the Equatorial Atlantic Ocean (0°-4°W). Cruise SOP 1, February 1979. A 14-day study with one station per day.

	Particulate carbon	Particulate nitrogen	Particulate phosphorus	Chlorophyll <u>a</u>	Phaeophytin <u>a</u>
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Table IV. Atomic ratios of the particulate organic matter in the chlorophyll maximum of the Equatorial Atlantic Ocean (0°-4°W). *3-35 μg is a calculated value. Cruise SOP I, February 1979

	C/N at/at	C/P at/at	N/P at/at	C/chla $\mu\text{g}/\mu\text{g}$
< 200 μm	8.2	122	15	133
< 35 μm	8.4	134	16	137
< 3 μm	9.1	181	20	200
3-35 μm^*	5.1	39	7.7	34.4

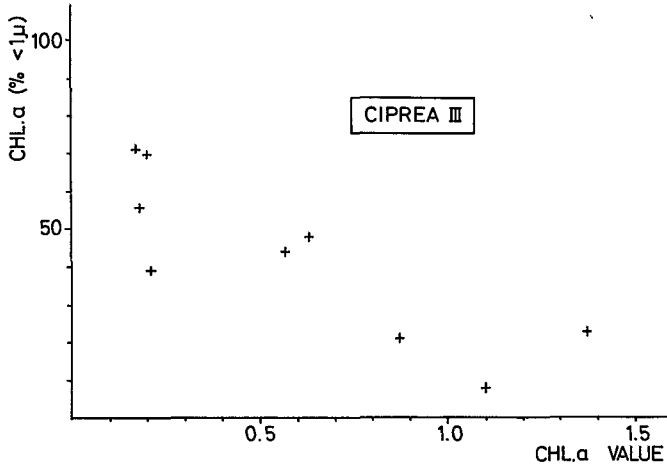


Fig. 3. Relationship between the chlorophyll a values ($\mu\text{g l}^{-1}$) and the percent of chlorophyll $< 1 \mu$ in the Gulf of Guinea waters.

have a higher proportion of large cells than the oligotrophic waters, or a lower proportion of detritus. Similar results were found with primary production data,

Table V. Size distribution of chlorophyll and phaeophytin in the superficial waters (stations 11, 14 and 20) and the thermocline waters (stations 22 and 34) during CIPREA II. The mean values (in $\mu\text{g l}^{-1}$) were not calculated since the stations are at different locations.

St	Depth (m)	Chlorophyll <i>a</i>								Phaeophytin <i>a</i>								Primary production								Phaeophytin rate			
		$\mu\text{g l}^{-1}$				%				$\mu\text{g l}^{-1}$				%				$\mu\text{gC l}^{-1} \text{ d}^{-1}$				%							
		<200	<35	<3	<1	<200	<35	<3	<1	<200	<35	<3	<1	<200	<35	<3	<1	<200	<35	<3	<1	<200	<35	<3	<1	<200	<35	<3	<1
9	5	0.171	0.182	0.154	0.121	100	106	90	70.8									-	-	-	-	-	-	-	-				
	50	0.182	0.185	0.154	0.101	100	102	84.6	55.5									-	-	-	-	-	-	-	-				
12	45	0.20	0.20	-	0.14	100	100	-	70.0	0.052	0.051	-	0.027	100	98.1	-	51.9	3.2	3.9	-	1.78	100	122	-	55.0	20.6	20.5	-	16.2
17	5	0.63	0.63	-	0.30	100	100	-	47.6	0.140	0.060	-	0.054	100	42.9	-	38.6	4.1	3.9	-	0.72	100	95.1	-	17.5	18.2	8.7	-	15.3
27	5	1.10	0.91	-	0.080	100	82.7	-	7.3	0.079	0.164	-	0.013	100	208	-	16.5	130.7	110.2	-	6.9	100	84.3	-	5.3	6.7	15.3	-	14.0
30	5	0.207	0.143	-	0.081	100	69.1	-	39.1	0.005	0.020	-	0.003	100	400	-	60	41.9	39.6	-	2.9	100	94.6	-	7.0	2.4	12.3	-	3.6
33	5	0.57	0.63	0.32	0.25	100	111	56	44	1.38	1.24	0.29	0.096	100	90	21	7.0	-	-	-	-	-	-	-	-	70.8	66.3	47.5	27.7
	1*	1.36	0.83	-	0.308	100	61	-	22.6	0.381	0.463	-	0.100	100	121.5	-	26.2	158.0	110.6	-	7.2	100	70.1	-	4.6	21.9	35.8	-	24.5
34	5	0.870	0.623	-	0.178	100	71.6	-	20.5	0.336	0.350	-	0.074	100	104	-	22.0	-	-	-	-	-	-	-	-	27.9	36.0	-	29.4

Table VI. Size distribution of chlorophyll, phaeophytin and primary production in the Equatorial upwelling. Cruise CIPREA III of RV Capricorne - July 1979. *Congo water.

St no	Depth (m)	chlorophyll <u>a</u>								phaeophytin <u>a</u>							
		$\mu\text{g l}^{-1}$				%				$\mu\text{g l}^{-1}$				%			
		<200	<35	<3	<1	<200	<35	<3	<1	<200	<35	<3	<1	<200	<35	<3	<1
11	5	0.196	0.160	0.130	0.110	100	82	66	56	0.024	0.025	0.025	0.021	100	104	104	87.0
14	0	0.169	0.172	0.100	0.090	100	102	59.2	53.2	0.023	0.025	0.027	0.024	100	109	117	104
20	0	0.069	0.054	0.050	0.047	100	78.3	72.5	68.1	0.015	0.014	0.012	0.015	100	93.3	80.0	100
		0.065	-	0.048	0.048	100	-	73.8	73.8	0.013	-	0.012	0.012	100	-	92.0	92
\bar{m}						<u>100</u>	<u>87.4</u>	<u>66.1</u>	<u>60.0</u>					<u>100</u>	<u>102</u>	<u>102</u>	<u>95.7</u>
σ						0	12.7	7.0	9.5					0	8.0	15.5	8.5
Cv						0	14.6	10.6	15.9					0	7.9	15.2	8.9
22	50	0.108	0.108	0.082	0.060	100	100	75.9	55.6	0.031	0.032	0.020	0.015	100	103	64.5	48.4
34	40	0.438	0.420	0.350	0.260	100	96	80	59.4	0.162	0.154	0.130	0.100	100	95	80.2	61.7
\bar{m}						<u>100</u>	<u>98</u>	<u>78</u>	<u>57.5</u>					<u>100</u>	<u>99</u>	<u>72.3</u>	<u>55.0</u>
σ						0	2.8	2.9	2.7					0	5.6	11.1	9.4
Cv						0	2.9	3.7	4.7					0	5.7	15.3	17.1

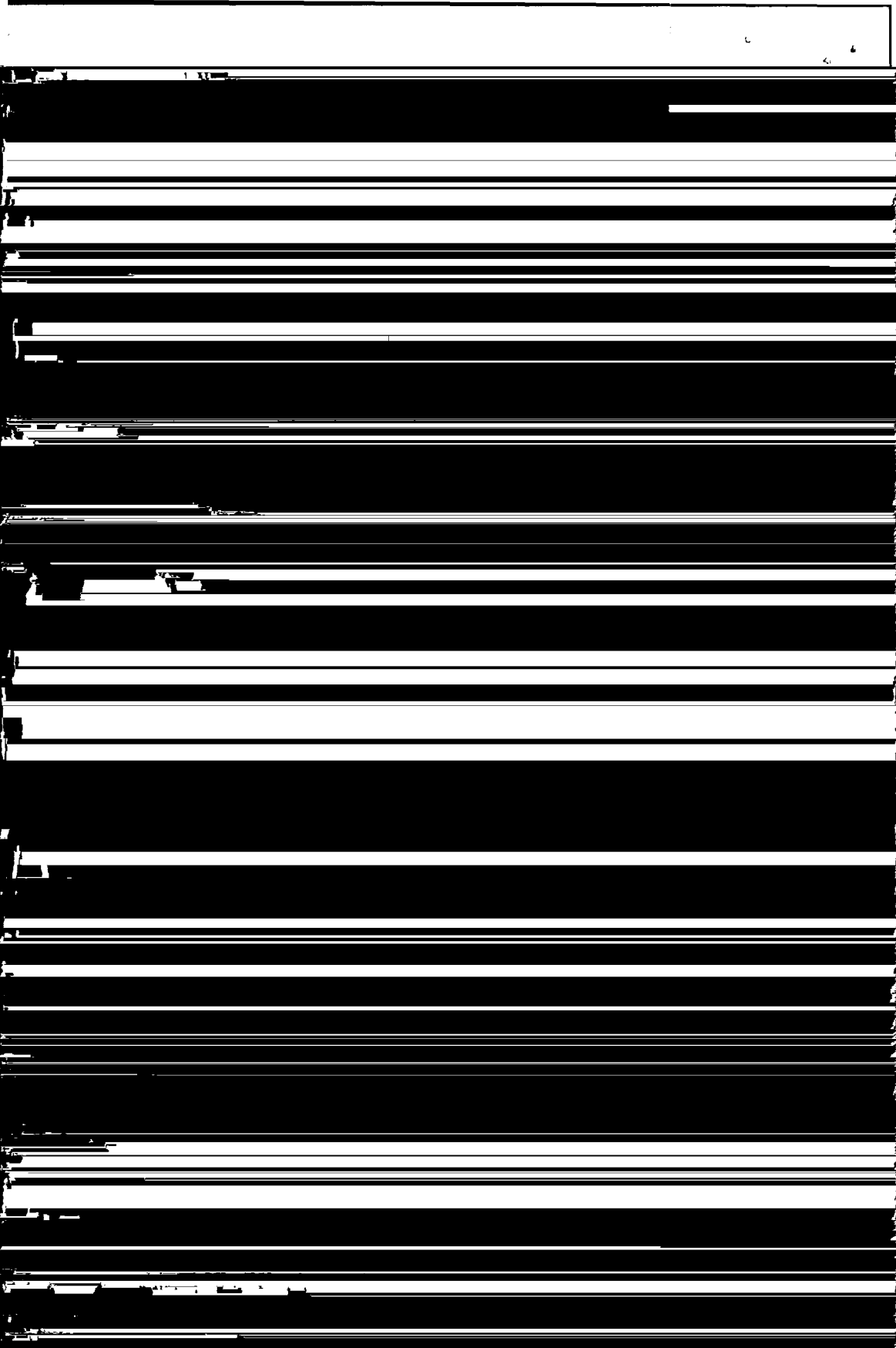
would be the physical damage during filtration on Nucleopore filters. No observation was made on the filtrate. But McCarthy *et al.* (1974) found no visual evidence of physical damage to athecate dinoflagellates filtered through a mesh somewhat smaller than the organisms, and Venrick *et al.* (1977) no evidence that any decline during their incubations was related to filtration; however, the taxa that declined the least were those with internal or external hard parts which may afford them some protection. In an experiment designed to minimize handling damage, the survival did not appear to be any greater than in other experiments.

abundance patterns (e.g. papers of Beers and Stewart, 1970 and Beers *et al.*, 1975) with relatively less effort being devoted to topics such as metabolic or trophic activities (Heinbokel, 1978). A large part of the microzooplankton populations includes forms with a relatively rapid rate of reproduction, generally by binary fission, and measurable in terms of hours: 24 hours for Ciliata other than Tintinnida and 48 hours for the Tintinnida are expected values (Beers *et al.*, 1975). In recent papers, Gieskes *et al.*, (1979), Postma and Rommets (1979), and Tijssen (1979) found unexpected high values of primary production in the Tropical Atlantic Ocean with three different methods. Estimation were so high that they practically obliterate the productivity difference between eutrophic and oligotrophic oceanic regions. In the tropical ocean, transfer of organic matter to higher food chains such as fish would be very restricted and probably the high productivity would be grazed and maintained (via excretion) by a very small standing stock of microplankton (Postma and Rommets, 1979), which turns quickly.

New ideas on limiting concentrations of nutrients for algal growth have recently been conceived (Goldman *et al.* 1979). They pointed out that even in the most oligotrophic parts of the ocean, enough nutrients for rapid, near maximal growth, are constantly being made available to algal cells through mineralization. Then, the rate processes in nutrient impoverished oceanic regions may be in a highly dynamic and balanced state. The extreme smallness of the particulate matter in these regions agrees well with these concepts.

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