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

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Abstract. The size fractionation of particulate matter (<200, <35, <3 and <1 μm) 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 $^{14}CO_2$ 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 μm Nucleopore filter, and 75-90% of the particulate carbon and nitrogen passed through 3 μm Nucleopore filter in offshore waters.

From the atomic ratio C/N, C/P and C/chla, and primary production values, the <3 μm 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 μm) and nanoplankton (<20-35 μm) 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 important primary producers in both neritic and oceanic environments, but netplankton productivity is higher in neritic than in oceanic waters (Malone, 1971 *b*).

In recent studies Berman, (1975) and Ibarra, (1978) found that a surprisingly high percentage of chlorophyll and photoautotrophic radioactivity appeared to pass through 5 μm or even 3 μm (Paerl and McKenzie, 1977). Some earlier studies have stressed the importance of ultraplankton (<5 μm). For example, Wauthy *et al.* (1968) found by an indirect method that numerous cells are probably not observed in the classic Utermöhl counting method, and Throndsen (1979) confirmed this result: "a few to more than 90% of marine phytoplankton is ultraplankton and may contribute equally much to the primary production". Burt (1958) applying the Mie theory of light scattering by particles to get a rough

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 analysis and assimilation studies.

Nutrients were determined by methods described in Strickland and Parsons (1972) with an autoanalyser (Technicon A II). For chlorophyll *a* measurements, 175 or 500 ml of sea water were filtered on glass fibre filters (Whatman GFC) under very low pressure ($\cong$75 mm Hg). After grinding and extraction (few hours) in 90% acetone, chlorophyll *a* was determined according to Yentsch and Menzel (1963) with a fluorometer (Turner III). Calibration of apparatus was made with pure chlorophyll *a* (Sigma) with a spectrophotometer.

For particulate organic matter analysis, 2 l of seawater were filtered on fibre glass filters (Gelman type A). Carbon and nitrogen analyses were run in a CHN analyser (Hewlett Packard 185 B) and particulate phosphorus was estimated by persulfate oxidation according to the method of Menzel and Corwin (1965).

Size fractionation: all samples were prefiltered through a 200 μm mesh net to remove the larger zooplankters. A 35 μm mesh net was used to separate netplankton from nanoplankton, and Nucleopore filters (3 μm and 1 μm nominal pore sizes) to separate the ultraplankton. Nucleopore filters are known to have a more uniform and precise pore size than cellulose-ester membrane filters and better screening characteristics (Sheldon, 1972; Chretiennot-Dinet, 1978).

As recommended by McCarthy *et al.* (1974), we have chosen a prescreening technique in primary production measurements: before incubation, samples of

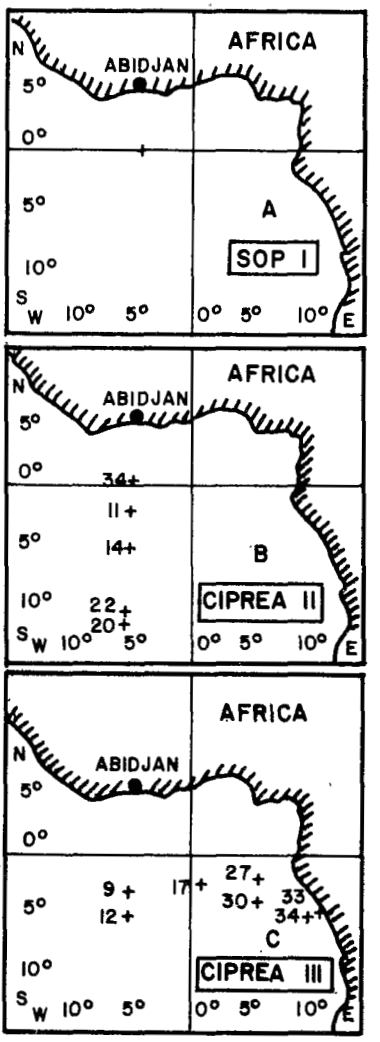

Fig. 1. Location of stations used in the study

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 $^{14}CO_2$ 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° ≅ 29°C) with quasi-undetectable nitrate and low values of chlorophyll *a* (= 0.10 $\mu g\ l^{-1}$). The thermocline is well developed. Chlorophyll *a* and primary production maxima are located above the nitrate gradient (= nitracline). Relative high

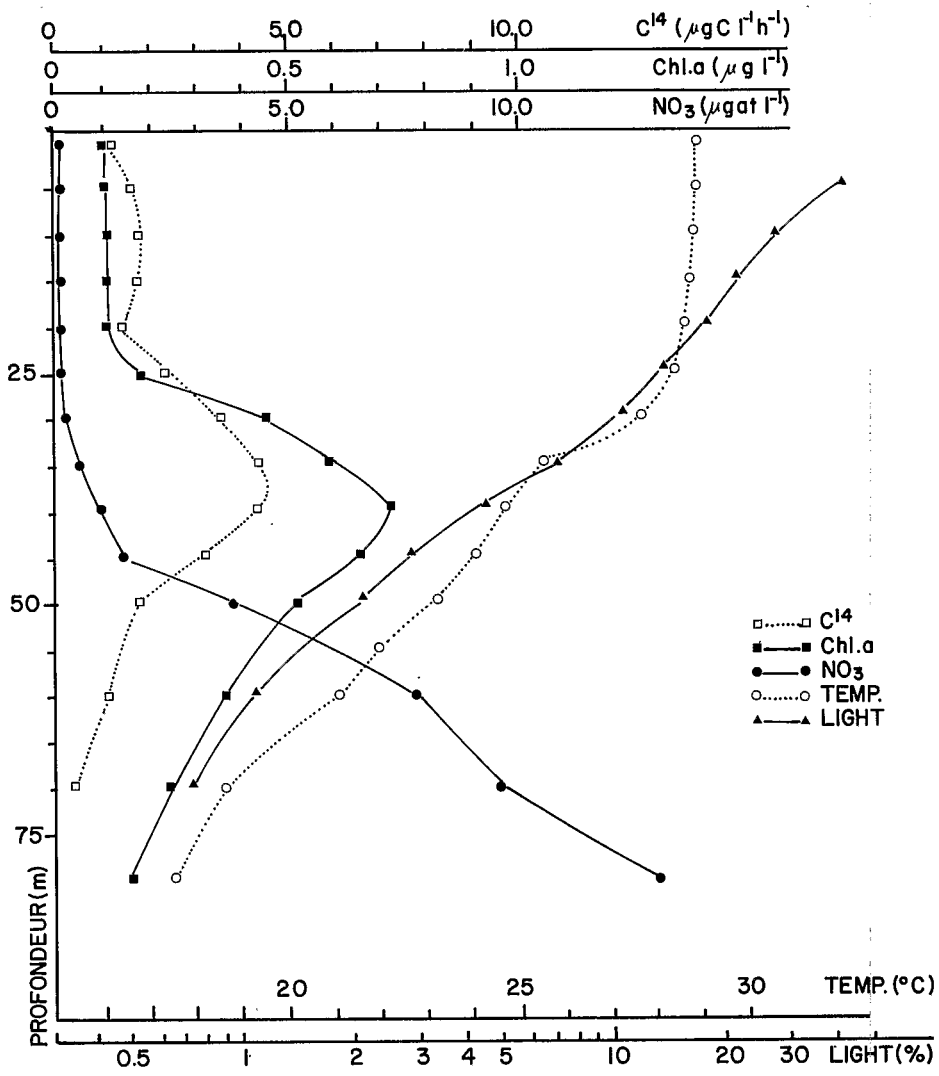

Fig. 2. The mean profiles of temperature, light, nitrate, chlorophyll *a* and $^{14}CO_2$ uptake during a long duration station (14 days) in the Equatorial Atlantic Ocean (0°-4° W). Cruise SOP 1.

values of chlorophyll ($\cong$ 1 $\mu g\, l^{-1}$) and primary production(5-7 $\mu gC\, l^{-1}\, h^{-1}$) 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 μm and 43% and 41% (mean values) through 3 μm. The proportion of chlorophyll in particles smaller than 3 μm is surprisingly high. The phaeophytin rate ([phaeophytin/(phaeophytin + chlorophyll a)] x 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 μm filtered water and only 20% by the 3 μm filtered water. It would mean that a high percentage of the photosynthetic active organisms have principally a size between 35 and 3 μm (70% of the total photosynthetic acitivity).

The Assimilation Number (AN = $\mu gC.\mu gchla^{-1}.h^{-1}$) are low in the <3 μm class (AN = 2.1) and higher in the 3-35 μm class (calculated value of AN = 11.2 - a very high value for oceanic waters, Table II).

The productivity estimates of the prescreened fraction is not easy to explain (Venrick *et al.*, 1977). A 35 μm screening removes a part of the phytoplankters and reduces the herbivore biomass and hence reduces the grazing rate within the bottles; then the comparison of primary productivity in a prescreened aliquot with that in an unscreened control is not simple. But the AN found in the 3-35 μm size class are less critical since the herbivore biomass is reduced both in <35 μm and <3 μm fraction, hence they can be compared between themselves.

During the second week of the 14 day study, the size distribution of particulate carbon, nitrogen and phosphorus was investigated. The results are summarized in Table III.

Nearly all the particulate carbon and nitrogen are smaller than 35 μm (96.4 and 97%); the percentages exceeding 100% are not significant and are probably due to imprecision in the method. For carbon and nitrogen the <3 μm fraction is again high: 86.4 and 79.1% respectively (mean values), whereas it is less for phosphorus (60.5%), chlorophyll (58.4%) and phaeophytin (54.7%).

From the comparison between Table I and Table III, we can see that the chlorophyll bearing organisms are smaller in the second week than in the first, and the values of particulate organic matter decrease during the second week. These changes seem to be associated with the south-north oscillations of the current system and have been studied in a previous paper (Herbland and le Bouteiller, in press).

The C/N, C/P, N/P and C/chl *a* ratios mean values in the different size classes are presented in Table IV.

In the <3 μm class, the high ratio values are characteristic of detritus: C/N = 9, C/P = 181 and C/chla = 200 with low content of phosphorus and chlorophyll. On the other hand, the calculated values for the 3-35 μm size class are near

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

St	chlorophyll a						phaeophytin a						^{14}Carbon uptake						Ass Number			Phaeophytin rate		
	$\mu g\ l^{-1}$			%			$\mu g\ l^{-1}$			%			$\mu gC\ l^{-1}\ h^{-1}$			%			$\mu gC\ \mu gchla\ h^{-1}$			%		
	<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° - 4°W). Cruise SOP 1, February, 1979.

	chlorophyll *a* $\mu g\ l^{-1}$	phaeophytin *a* $\mu g\ l^{-1}$	^{14}C uptake $\mu gC\ l^{-1}h^{-1}$	A.N. $\mu gC\ \mu gchla^{-1}h^{-1}$	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% (σ = 9.5) of the chlorophyll passed through the 1 μm Nucleopore filter in the mixed layer waters (0 and 5 m) and 57.5% (σ = 2.7) in the thermoclinal 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. Chla 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 chla, values between 0.005 $\mu g\ l^{-1}$ and 0.01 are commonly found for phaeophytin. If they are not subtracted to the samples values, the phaeophytin will be overestimated.

The last set of results was obtained during the CIPREA III cruise, covering a large area in the Gulf of Guinea (Figure 1C), when the Equatorial upwelling is active (Voituriez and Herbland, 1977). During that cruise a large range of chlorophyll *a* values were measured (from 1.36 $\mu g\ l^{-1}$ in the Congo waters, to 0.17 $\mu g\ l^{-1}$ in the central part of the Gulf of Guinea (st. 9). We found a negative relationship between the chlorophyll *a* values and the <1 μm size fraction (Figure 3). Since chlorophyll *a* appears in both x and y variables no statistical test of correlation was attempted; but it is obvious that the variations of y (y = chl *a* <1 μm/chl *a*) are not only due to the variations of x (x = chl *a*) since the numerator of y varies four-fold (see Table VI). It confirms that the most productive areas

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.

St	Particulate carbon						Particulate nitrogen						Particulate phosphorus						Chlorophyll a						Phaeophytin a					
	μgat l^{-1}			%			μgat l^{-1}			%			μgat l^{-1}			%			μg l^{-1}			%			μg l^{-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	<200	<35	<3	<200	<35	<3
6	9.61	7.51	6.40	100	78	67	1.35	0.85	0.75	100	63	56							1.08	0.83	0.53	100	77	49	0.53	0.45	0.32	100	85	60
8	8.16	8.50	7.53	100	104	92	0.96	1.00	0.75	100	104	78	74	60	42	100	81	57	0.97	0.97	0.50	100	100	51	0.54	0.52	0.29	100	96	54
9	8.12	7.13	7.54	100	88	93	1.01	0.85	0.87	100	84	86	73	57	40	100	78	55	0.64	0.55	0.39	100	86	62	0.55	0.44	0.19	100	80	35
10	7.89	6.88	6.62	100	87	84	0.82	0.83	0.74	100	101	90	57	50	42	100	88	74	0.53	0.58	0.34	100	108	64	0.39	0.24	0.19	100	62	49
11	6.75	6.88	6.13	100	102	91	0.82	0.84	0.68	100	102	83	69	51	36	100	74	52	0.56	0.58	0.37	100	104	66	0.44	0.42	0.23	100	95	52
12	5.43	5.79	4.74	100	106	87	0.64	0.76	0.52	100	118	81	54	55	29	100	102	54	0.44	0.41	0.25	100	92	57	0.36	0.33	0.23	100	92	54
13	4.64	5.10	4.21	100	110	91	0.54	0.58	0.43	100	107	80	28	32	20	100	114	71	0.33	0.27	0.20	100	80	60	0.19	0.17	0.15	100	89	79
m	7.23	6.83	6.17	100	96.4	86.4	0.88	0.81	0.68	100	97.0	79.1	59	51	34.8	100	89.5	60.5	0.65	0.60	0.37	100	92.4	58.4	0.43	0.37	0.23	100	85.6	54.7
σ	1.73	1.11	1.28	0	12.0	9.1	0.27	0.13	0.15	0	18.0	11.0	17.4	9.9	8.8	0	15.5	9.5	0.27	0.24	0.12	0	12.0	6.5	0.13	0.12	0.06	0	11.8	13.2
Cv	24	16	20.8	0	12.4	10.6	30.3	16.3	22.4	0	18.6	13.8	29.4	19.6	25.2	0	17.3	15.7	42.0	39.7	32.7	0	13.0	11.0	30.2	34.2	26.1	0	13.8	24.1

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 1, February 1979

	C/N at/at	C/P at/at	N/P at/at	C/chla μg/μg
<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

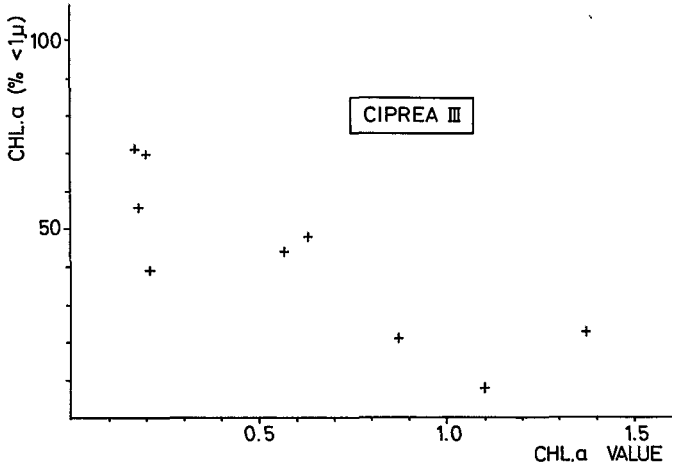

Fig. 3. Relationship between the chlorophyll *a* values ($\mu g l^{-1}$) and the percent of chlorophyll <1 μ in the Gulf of Guinea waters.

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, where the higher values of $^{14}CO_2$ uptake (st. 27, 30 and 34) correspond to lower values of the <1 μm class (5.3, 7 and 4.6% respectively, Table VI).

In conclusion, a high proportion of particulate organic matter would be smaller than 1 μm in the offshore waters of the Eastern Tropical Atlantic Ocean. The extreme smallness of the heterotrophic organisms responsible for dissolved organic matter uptake is well known and not surprising (Williams, 1970; Berman, 1975) since bacteria are the smallest living organisms (virus excepted). But the smallest photosynthetic planktonic alga known is *Micromonas pusilla* which has a diameter of 0.8 μm; then it is unlikely that the chlorophyll *a* which passes through the 1 μm filter is mainly supported by living phytoplankton cells.

Other data on size fractionation in the Tropical Atlantic Ocean are few. As far as we know, two studies have been published: Ibarra (1978) in the Guinea Dome and Gieskes *et al.* (1979) in the North Equatorial current. Their results agree with ours since Ibarra found that 69% of the chlorophyll *a* passed through 5 μm Nucleopore filters and Gieskes *et al.* 62.5% through 3 μm and 48% through 1 μm unipore filters.

Such high percentages of small particles may be suspicious. A possible cause

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

St	Depth(m)	Chlorophyll a $\mu g\ l^{-1}$				Chlorophyll a %				Phaeophytin a $\mu g\ l^{-1}$				Phaeophytin a %				Primary production $\mu gC\ l^{-1}\ d^{-1}$				Primary production %				Phaeophytin rate			
		<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
34	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
	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 a								phaeophytin a							
		$\mu g\ l^{-1}$				%				$\mu g\ l^{-1}$				%			
		<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
$\bar{m}$						100	87.4	66.1	60.0					100	102	102	95.7
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
$\bar{m}$						100	98	78	57.5					100	99	72.3	55.0
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, but they prudently concluded that "a single experiment is inadequate for a firm conclusion".

Conclusions

It is well-known that the cell size of the primary producers and detritical particles play important roles in phytoplankton population dynamics (Banse, 1976) and trophic interactions in the marine ecosystems (Ryther, 1969; Martin, 1970; Conover, 1978).

The particulate organic matter measured as carbon, nitrogen, phosphorus and chlorophyll exhibit very small sizes in the offshore waters of the Equatorial Atlantic Ocean. It appears from simultaneous measurements of primary production that the smaller fraction (<3 and 1 μm) is mainly constituted by inactive photosynthetic organisms; but a measurable photosynthetic activity exists in that fraction. Since the prescreening technique used in this study reduces the possibility of breakage during final filtration, it is likely that very small (< 1 μm) photosynthetic algae exist in these waters. Recently, with transmission electron micrographs, Sieburth showed that both procaryotes and eucaryotes smaller than 1 μm were found in natural samples of sea water (Comm. at PRPOOS workshop, San Diego, 1981). The recent method of numeration of bacteria by epifluorescence (Zimmerman and Meyer-Reil, 1974) revealed an unexpected high number of very small bacteria (<0.5 μm) not visible by previous techniques. From the values of atomic ratio on the different size classes, it seems that the proportion of detritical particles increases when the size decreases.

Methodological consequences of the extreme smallness of the seston in these waters would be (1) the use of Whatman GFC and Gelman type A filters is not to be recommended; a significant fraction passes through that filters (Herbland, unpublished data) and it is likely that the so-called "Soluble Fluorescence" measured in the equatorial waters of the tropical Atlantic Ocean by Herbland (1978) may be in part, due to ultraphytoplankton incompletely removed (Parker, 1981); (ii) prescreening with 100 μm, even 50 μm mesh size (instead of 200 μm) could be undertaken to obtain a better separation between phytoplankton and herbivores in studies with incubations.

The main ecological consequence is that our ideas on the structure of the food webb may be a little modified. The filtration efficiency of copepods is very low under 3 μm (Nival and Nival, 1976) even for first copepodite stages of the small *Acartia*. By what kind of organisms are these small particles eaten? Does microplankton play a more important role than was believed? Most of the research on the microzooplankton (<200 μm) has been devoted to define distribution and

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.

References

Anderson,G.C., 1965: 'Fractionation of phytoplankton communities off the Washington and Oregon coasts'. *Limnol. Oceanogr.*, **10**, 477-480.

Antia,N.J., C.D.McAllister, T.R.Parsons, K.Stephens and J.D.H.Strickland. 1963: 'Further measurements of primary production using a large volume plastic sphere'. *Limnol. Oceanogr.*, **8**, 166-183.

Azam,F. and O.Holm-Hansen, 1973: 'Use of tritiated substances in the study of heterotrophy in sea water.' *Mar. Biol.*, **23**, 191-196.

Banse,K., 1976: 'Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size - a review.' *J. Phycol.*, **12**, 135-140.

Beers,J.R. and G.L.Stewart, 1970: 'Numerical abundance and estimated biomass of microzooplankton. *Bull. of the S.I.O.*, **17**, 58-78.

Beers,J.R., F.M.H.Reid and G.L.Stewart, 1975: 'Microplankton of the North Pacific Central Gyre. Population, structure and abundance, June 1973.' *Int. Revue ges. Hydrobiol.*, **60**, 607-638

Berman,T., 1975: 'Size fractionation of natural aquatic populations associated with autotrophic and heterotrophic carbon uptake.' *Mar. Biol.*, **33**, 215-220

Burt,W.V., 1958: 'Selective transmission of light in tropical Pacific waters.' *Deep Sea Res.*, **5**, 57-61.

Chretiennot-Dinet,H.J. and E.Vacelet, 1978: 'Separation fractionnée du phytoplancton et estimation de l'assimilation autotrophe et hététrophe de ^{14}C'. *Oceanologica Acta,* **1**, 407-413.

Conover,R.J., 1978: 'Transformation of organic matter' in *Marine Ecology,* vol 4, Ed by O.Kinne, pp 221-499

Durbin,E.G., R.W.Krawiec and T.J.Smayda, 1975: 'Seasonal studies on the relative importance of different size fractions of phytoplankton in Narragansett Bay (USA).' *Mar. Biol.*, **32**, 271-287.

Eppley,R.W. and P.R.Sloan, 1966: 'Growth rates of marine phytoplankton: correlation with light and absorption by cell chlorophyll a.' *Physiol. Plant.*, **19**, 47-59.

Gieskes,W.W.C., G.W.Kray and M.A.Baars, 1979: 'Current ^{14}C methods for measuring primary production: gross underestimates in oceanic waters.' *Neth. J. of Sea Research.*, **13**, 58-78.

Gilmartin,M., 1964: 'The primary production of British Columbia fjord.' *J. Fish. Res. Bd Can.*, **21**, 505-538.

Heinbokel,J.F., 1978: 'Studies on the functional role of tintinnids in the southern California Bight. I. Grazing and growth rates in laboratory cultures.' *Mar Biol.*, **47**, 177-189.

Herbland,A., 1978: 'The soluble fluorescence in the open sea: distribution and ecological significance in the equatorial Atlantic Ocean.' *J. Exp. Mar. Biol. Ecol.*, **32**, 275-284

Herbland,A. and B.Voituriez, 1979: 'Hydrological structure analysis for estimating the primary production in the Tropical Atlantic Ocean.' *J. Mar. Res.*, 37 pp.

Herbland,A. and A.le Bouteiller (in press): 'The meanders of equatorial current: influence on the biological processes.' *Oceanogr. Tropical.*

Holmes,R.W., 1958: 'Surface chlorophyll a, surface primary production and zooplankton volumes in the Eastern Pacific Ocean.' *Rapp. P.V. Réun. Cons. Perm. Int. Expl. Mer,* **144**, 109-116.

Ibarra,S.E., 1978: 'Rôle des différentes catégories de taille dans les processus auto et hétérotrophiques en milieu pélagique.' *Thése doc. 3éme cycle, Univ. de Paris VI,* 142 p.

Malone,T.C., 1971*a:* 'The relative importance of nanoplankton and netplankton as primary producers in the California current system.' *Fish Bull.*, **69**, 799-820.

Malone,T.C., 1971*b:* 'The relative importance of nanoplankton and netplankton as primary producers in tropical oceanic and neritic phytoplankton communities.' *Limnol. Oceanogr,* **16**, 633-639.

Malone,T.C., M.B.Chervin and D.C.Doardman, 1979: 'Effects of 22 μm screens on size frequency distributions of suspended particles and biomass estimates of phytoplankton size fractions.' *Limnol. Oceanogr.*, **24**, 956-960.

McAllister,C.D., T.R.Parsons, K.Stephens and J.D.H.Strickland, 1961: 'Measurements of primary production in coastal sea water using a large volume plastic sphere.' *Limnol. Oceanogr.*, **6**, 237-258.

McCarthy,J.J., W.R.Taylor and M.E.Loftus, 1974: 'Significance of nanoplankton in the Chesapeake Bay Estuary and problems associated with the measurements of nanoplankton productivity.' *Mar. Biol.*, **24**, 7-16.

Martin,J.H., 1970: 'Phytoplankton-zooplankton relationships in Narragansett Bay. IV. The seasonal importance of grazing.' *Limnol. Oceanogr.*, **15**, 413-418.

Menzel,D.W. and N.Corwin, 1965: 'The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxydation:' *Limnol. Oceanogr.*, **10**, 280-282.

Nival,P. and S.Nival, 1976: 'Particle retention efficiencies of an herbivorous copepod, *Acartia clausi* (adult and copepodite stages): effects on grazing.' *Limnol. Oceanogr.*, **21**, 24-38.

Paerl,H.W. and L.A.Mackenzie, 1977: 'A comparative study of the diurnal fixation patterns of nanoplankton and netplankton.' *Limnol. Oceanogr.*, **22**, 32-738.

Parker,R.R., 1981: 'A note on the so-called "soluble fluorescence" of chlorophyll *a* in natural waters. *Deep Sea Research,* (in press).

Parsons,T.R. and R.J.Lebrasseur, 1970: 'The availability of food to different trophic levels in the marine food chain.' pp 325-343. In J.H.Steele (ed.), *Marine Food Chains.* Oliver & Boyd.

Postma,H. and J.W.Rommets, 1979: 'Dissolved and particulate organic carbon in the North Equatorial current of the Atlantic Ocean.' *Neth. J. Sea. Res.*, **13**, 85-98.

Ryther,J.H., 1969: 'Photosynthesis and fish production in the Sea.' *Science,* **166**, 72-76.

Sheldon,R.W., 1972: 'Size separation of marine seston by membrane and glass fibre filters.' *Limnol. Oceanogr.*, **17**, 494-498.

Steemann Nielsen,E. and E.A.Jensen, 1957: 'Primary oceanic production, the autotrophic production of organic matter in the ocean.' *Galathea Rep.*, **1**, 49-136.

Strickland,J.D.H. and T.R.Parsons, 1972: 'A practical hand book of seawater analysis.' *Bull. Fish. Res. Bd Can.*, **167**, 311 p.

Teixeira,C., 1963: 'Relative rates of photosynthesis and standing stock of netphytoplankton and nanoplankton.' *Bolm. Inst. Oceanogr., S. Paulo* **13**, 53-60.

Throndsen,J., 1979: 'The significance of ultraplankton in marine primary production'. *Acta Bot. Fennica,* **11**, 53-56.

Tijssen,S.B., 1979: 'Diurnal oxygen rhythm and primary production in the mixed layer of the Atlantic Ocean at 20°N.' *Neth. J. Sea. Res.* **13**, 79-84.

Venrick,E.L., J.R.Beers and J.F.Heinbokel, 1977: 'Possible consequences of containing microplankton for physiological rate measurements.' *J. Exp. Mar. Biol. Ecol.*, **26**, 55-76.

Voituriez,B. and A.Herland, 1977: 'Etude de la production pélagique de la zone équatoriale de l'Atlantique à 4°W. Relations entre la structure hydrologique et la production primaire.' *Cah. ORSTOM, sér. Océanogr.*, **15**, 313-332.

Walsh,J.J., 1976: 'Herbivory as a factor in patterns of nutrient utilization in the sea.' *Limnol. Oceanogr.*, **21**, 1-13.

Wauthy,B., R.Desrosieres and J.Lebourhis, 1968: 'Importance présumée de l'ultraplankton dans les eaux tropicales du Pacifique Central Sud. *Cah. ORSTOM, sér Océanogr.*, **5**,

Williams,R.B., 1964: 'Division rates of salt marsh diatoms in relation to salinity and cell size.' *Ecology*, **45**, 877-880.

Williams,P.J., Le,B., 1970: 'Heterotrophic ultilization of dissolved organic compounds in the sea. I. Size distribution of population and relationship between respiration and incorporation of growth substrates.' *J. Mar. Biol. Ass. U.K.*, **50**, 859-870.

Yentsch,C.S. and J.H.Ryther, 1959: 'Relative significance of the net phytoplankton and nanoplankton in the waters of Vineyard Sound.' *J. Cons. Int. Explor. Mer*, **24**, 231-238.

Yentsch,C.S. and D.W.Menzel, 1963: 'A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence.' *Deep Sea Res.*, **10**, 221-231.

Zeitzschel,B., 1970: 'The quantity, composition and distribution of suspended particulate matter in the Gulf of California.' *Mar. Biol.*, **7**, 305-318.

48