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Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu archipelago)

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Abstract

Suspended particulate matter was comprehensively investigated from 6 to 17 April 1986 in the lagoon of Tikehau atoll (15°00'S; 148°10'W). Dry weight (DW), particulate organic carbon (POC), adenosine triphosphate (ATP), and chlorophyll a were measured for five size-classes (0.2 to 0.8 μm, 0.8 to 3 μm, 3 to 35 μm, 35 to 200 μm, and 200 to 2 000 μm). Taxa were identified and counted for the whole plankton (both autotrophic and heterotrophic). Particles <3 μm accounted for 81% of the total POC (192 mg m^{-3}), and detritus comprised 82% of the total POM. Phytoplankton (cyanobacteria plus algae) accounted for 35% of the living carbon, 75% of which consisted of heterotrophic bacteria and cyanobacteria. The zooplankton biomass was composed of 31% nano-, 26% micro-, and 43% mesoplankton.

Introduction

A study of the structure of the lagoon ecosystem of the atoll of Tikehau was carried out during the ATOLL program of the ORSTOM Center in Tahiti. Earlier studies (Charpy et al. 1986) had revealed the particulate organic matter (POM) to contain a large amount of detritus and a small amount of phytoplankton. Further measurements and analyses have now enabled us to determine the particulate fraction quantitatively and qualitatively, and to add observations on size classes >35 μm. In order to construct a model of the pelagic food-web in the lagoon of the atoll, we divided seston particles >0.2 μm into various size-classes. Although a number of earlier studies have investigated the amounts of particulate substances entering a lagoon from a reef and have considered their fate (Johannes 1967, Marshall 1968, Qasim and Sankaranarayana 1970, Coles and Strathmann 1973), very few have dealt with the smallest particle fraction. Mention must, however, be made of the study by Gerber and Marshall (1982), which provides an exhaustive description of suspended particulate matter (detritus, phytoplankton and zooplankton) and of feeding by zooplankton.

In a coral atoll environment, the absence of terrigenous inputs means that the system is dependent on the surrounding open ocean for nutrient supply, and nutrient regeneration is therefore of primary importance.

Our study examines the different components of the organic seston, i.e., all particles >0.2 μm suspended in the water, including both plankton made up of living organisms, and tripton composed of non-living particles. Particulate organic carbon (POC) was weighed and analysed in each size class. Living particulate organic matter (LPOM) was measured by conversion of ATP into living carbon, and phytoplankton by chlorophyll measurement. The floral and faunal composition, abundance (numbers and biomass), and size-class structure of the plankton from 0.2 to 2 000 μm were determined by microscopy.

Materials and methods

The study site is the open atoll of Tikehau, lying at the western part of the Tuamotu archipelago (15°00'S; 148°10'W). A description of the atoll has been given by Intes (1984).

Sampling

On the basis of previous research on particulate organic matter in the lagoon of Tikehau (Charpy et al. 1986), the Faufaa station (No. 6 in Fig. 1) was regarded as being representative of the lagoon as a whole, and samples were collected there over a period of 11 d in April 1986. The station is 3 km from the laboratory in Tuherahera motu. It is not directly affected by the open sea or by the barrier reef, being a good distance from the reef and from the pass. Its position is marked by a fixed buoy and the depth of the water column is 19 m.

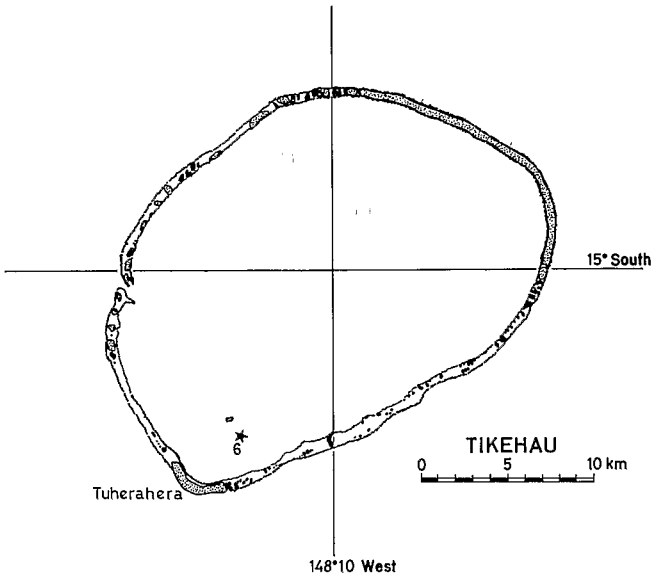

Fig. 1. Tikehau atoll, Tuamotu archipelago, showing location of Station 6

All samples used for counts were collected in the daytime, around 17.00 hrs. Particles <35 μm were carefully sampled at the surface, passed through a 35 μm-mesh gauze, and store in an ice box. During transport, they were kept in the dark to avoid deterioration of the chlorophyll pigments. Particles in the 35 to 200 μm size-class were collected with a 35 μm-mesh net hauled vertically from the bottom to the surface at a maximum speed of 33 cm s^{-1}. The characteristics of this cylindroconical net, which filtered the water without clogging, were: mouth diam = 33.5 cm, bottom diam = 10.0 cm, length = 3.30 m. The volume of water filtered was measured with a Tsurumi-Seiki-Kosakusho Co. mechanical flowmeter; the calculated volumes and the measured volumes were very similar, indicating a filtration efficiency of ca. 100. The particles were sieved through a 200 μm-mesh gauze and then put into an ice-box. Particles >200 μm were collected with a cylindroconical WP 2 net (mouth diam = 57.0 cm, bottom diam = 10.0 cm, length = 2.61 m; Anonymous 1968) hauled vertically from the bottom to the surface. The particles retained were then sieved through a 2 mm metal grid.

Weighing and analyses

Dry weights were measured on preweighed Whatman GF/F glass microfibre filters (25 mm diam) for particles <35 μm, and on preweighed gauze for the other fractions. The samples had been previously dried at 60 °C for 24 h by the method of Le Borgne (1975). The glass microfibre filters were rinsed with HCl (1 *N*), then burned at 500 °C for 4 h to remove any trace of organic matter. Particles <35 μm were weighed on a Cahn electrobalance with a reading precision of 1 μg, particles >35 μm on Mettler scales with a reading precision of 0.1 mg.

POM was obtained directly for particles >200 μm by the ash-free dry weight method, whereby preweighed samples are burned at 550 °C for 1.5 h, and the ash is allowed to cool off to normal room temperature before weighing (Le Borgne 1975).

Chemical analyses

Chemical analyses were performed twelve times, on samples collected at the surface and at depths of 5, 10, and 15 m for the <35 μm fraction, and on seven samples collected by net along the whole water column for the 35 to 200 μm and 200 to 2 000 μm fractions.

For carbon analysis, we used a CHN Hewlett-Packard 185 B analyser at 720 °C to minimize carbonate interference on the filters for particles <35 μm (Gordon and Sutcliffe 1973), and at 1 100 °C on diluted homogenates for the larger particles (Le Borgne 1975). The carbon content of particles <3 μm was determined after filtration on 3 μm Nuclepore filters. Values for the 3 to 35 μm fraction were obtained by subtraction (carbon content of 0.7 to 35 μm particles minus carbon content of 3 to 35 μm particles).

Chlorophyll *a* and pheopigments for plankton <35 μm were determined after filtration of 100 to 300 ml water on a Whatman GF/F glass microfibre filter; for this fraction, and for the 35 to 200 μm phytoplankton fraction collected by the net we used the method of Yentsch and Menzel (1963). ATP was analysed both for particles <35 μm (after filtration of 250 to 500 ml of water through a Millipore HA 0.45 μm filter) and for particles >35 μm, collected by the plankton net. Extraction was performed immediately with boiling Tris by the method of Holm-Hansen and Booth (1966). In the absence of an actual measured value for C:ATP plankton in Tikehau, we used C:ATP=250 for particles <35 μm (Hamilton and Holm-Hansen 1967) and an arbitrary choice of C:ATP=125 for particles >35 μm.

Microscopy

Within 30 min of collection, the samples were preserved with formaldehyde buffered by addition of sodium tetraborate (pH=8.5). The concentration of preservative used varied with the size of the particles, being 1% for pico- and nanoplankton (<35 μm fraction), 5% for microzooplankton (35 to 200 μm fraction) as recommanded by Beers and Stewart (1969), and 10% for mesozooplankton (200 to 2·000 μm fraction).

Identification and counting of pico- and nanoplankton <35 μm were performed using a Wild-Leitz Dialux microscope with a Ploemopak turret equipped with Filters A (340 to 380 nm) and I_2 (450 to 490 nm) for epifluorescence observation. An HBO50 light source was used. The procedure was based on that developed by Sherr and Sherr (1983), and consisted of double-staining with 4′, 6-diamidine-2-phenyl-

Table 1. Procedure used for counting autotrophic picoplankton, and autotrophic and heterotrophic nanoplankton by epifluorescence microscopy. DAPI: 4',6diamidino-2-phenylindole; FITC: fluorescein isothiocyanate

Taxa	Cyanobacteria	Phytoplankton	Heterotrophic flagellates	Ciliates
Buffered formaldehyde (‰)	0.5–1	0.5–1	0.5–1	0.5–1
No. of sub-samples	3	3	3	3
Vol of sub-samples (ml)	1–5	50	50–100	100–200
Staining	0	DAPI+FITC	DAPI+FITC	DAPI+FITC
Nucleopore pore-size (μm)	0.2	0.8	0.8	0.8
No. of fields counted	20–60	100	100–200	100–200
Min. no of organisms counted per sub-sample	1 600	600	100	50
Lens used	100	100	100	40
Magnification	1 560×	1 560×	1 560×	625×

indole, DAPI (for nuclei identification), and fluorescein isothiocyanate, FITC (for protein identification). The procedure is summarized in Table 1. The volumes filtered ranged from 1 to 200 ml, depending on the nature and size of the organisms. A 0.2 μm Nuclepore filter was used for cyanobacteria, and a 0.8 μm filter for the other organisms. The efficient surface area of the filters was estimated from the mouth diameter of the lower end of the filtration funnel. The surface of the observation fields was estimated from the supplier's specifications and checked with a micrometer.

The number (N) of organisms per ml of water was calculated using

$$N = \frac{n \cdot ncf}{ncc \cdot V}, \quad (1)$$

where n is the number of organisms, counted, ncf the number of fields per filter, ncc the number of fields observed, and V the volume of water filtered (Sherr and Sherr 1983). The size of the organisms and their cell volume were determined by the method of Beers and Stewart (1969), which consists of measuring the size of about 20 organisms of each taxon and estimating the mean volume per individual.

Microplankton (35 to 200 μm) was observed with an inverted microscope, after separation of the samples by sieving into two size-classes (A, 35 to 100 μm; B, 100 to 200 μm). For the major taxa, we took into account the recommendations of Lund et al. (1958), namely that a count of 100 organisms leads to an accuracy of ±20% at the 95% confidence level, and a count of 400 organisms to an accuracy of ±10%, assuming random distribution. In our case, these quantities corresponded to subsamples ranging from one-tenth to one-fortieth of the total sample. We have reported numerical abundance for the minor taxa, but these estimations are very uncertain. In order to obtain good estimates, the whole sample would have had to be counted.

Mesozooplankton (200 to 2 000 μm) was observed with a dissecting microscope. The whole sample was counted, except for copepods, which were counted from an aliquot obtained by suction (Frontier 1972) and containing at least 500 individuals.

Table 2. Dry weight (DW), particulate organic carbon (POC), ATP and chlorophyll *a* (Chl. *a*) in different particle size-classes of seston. Values are mg m^{-3}, with percentages of total in parentheses

Size class (μm)	DW	POC	ATP	Chl. *a*
0.7–3	1 652 (79.2)	146.6 (76.2)	0.114 (71.9)	0.228 (90.2)
3–35	395 (18.9)	35.0 (18.2)	0.012 (7.6)	0.024 (9.6)
35–200	21 (1.0)	3.9 (2.0)	0.012 (7.7)	0
200–2 000	19 (0.9)	7.0 (3.6)	0.020 (12.8)	0
Total	2 087	192.5	0.158	0.252

Results

Weight distribution of seston components by size-class

Virtually the whole of the seston, in terms of dry weight, was comprised of particles passing through a 35 μm sieve (98%: see Table 2). If one considers the directly measured values of carbon, ATP and chlorophyll *a*, components common to all the size-classes, it is obvious that nearly 75% of POC and ATP were concentrated in the <3 μm fraction, which contained over 90% of the chlorophyll *a*.

Microscopy: identification and counting of plankton organisms by size-class

Fraction <35 μm (pico- and nanoplankton)

As no increase or decrease in numerical abundance was evident over the one-week period from 6–12 April (Fig. 2) we used mean values: 151 000 cyanobacteria (Cb) ml^{-1}, 2 100 microalgae (Phy) ml^{-1}, 71 heteroflagellates (Hfl) ml^{-1},

Table 3. Parameters of regression lines between numbers of cyanobacteria (Cb), phytoplankton other than cyanobacteria (Phy), heterotrophic flagellates (Hfl), and naked ciliates (Ci). $N=7$

Regression	Correlation coefficient	Slope of line	Height of line
Hfl/Ci	0.294	4.328	42.086
Hfl/Phy $\times 10^{-2}$	−0.376	−1.7	107.642
Hfl/Cb $\times 10^{-4}$	0.060	0.553	63.083
Ci/Cb $\times 10^{-4}$	−0.314	−0.230	10.018
Phy/Cb $\times 10^{-2}$	0.507	−1.029	36.847
Phy/Ci $\times 10^{+2}$	0.513	1.423	11.739

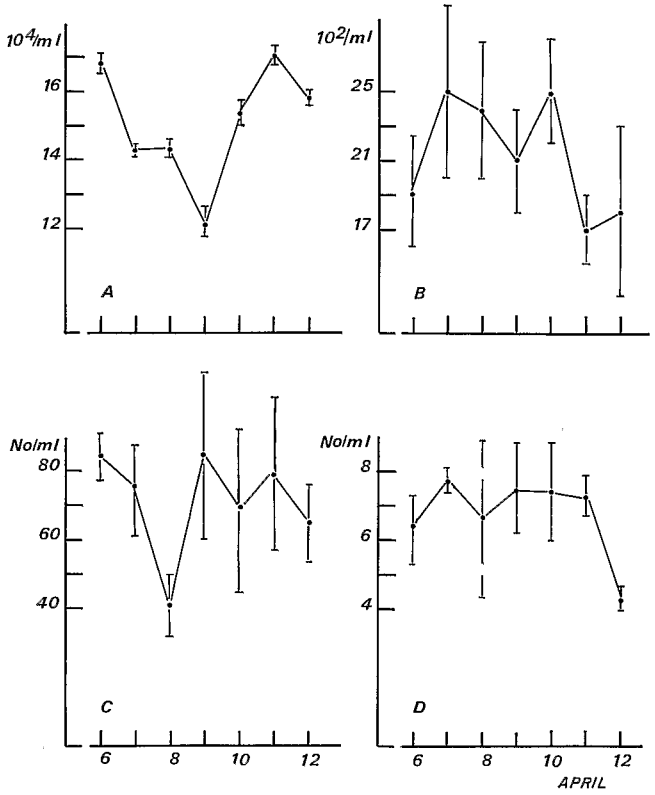

Fig. 2. Abundance of cyanobacteria (A), microalgae (B), heterotrophic flagellates (C), and ciliates (D) from 6 to 12 April 1986 at Tikehau atoll

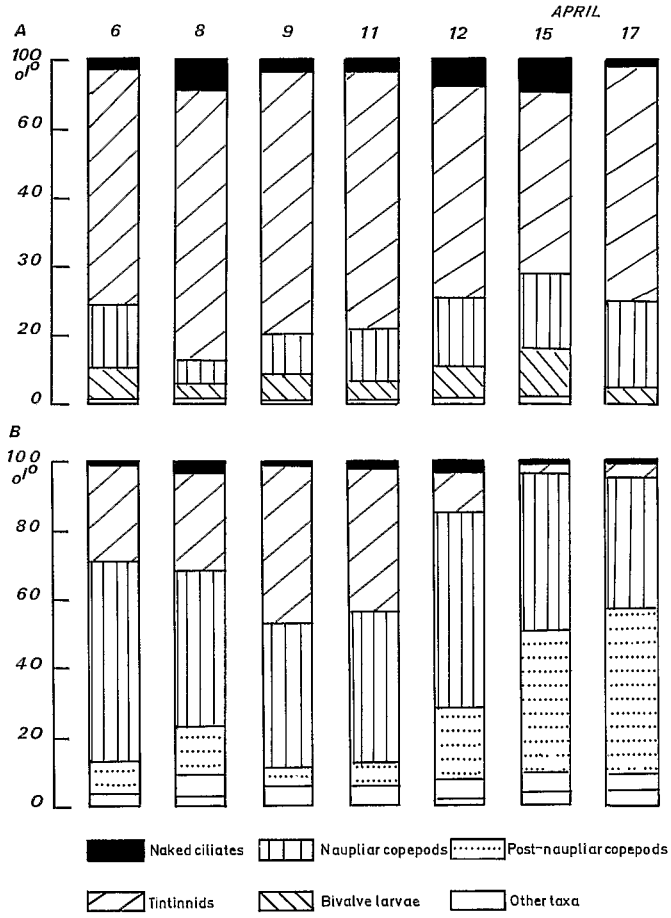

Fig. 4. Relatives percentages of microzooplankton numbers at Station 6 for Size Classes A (35 to 100 μm) and B (100 to 200 μm) on seven dates April 1986

and 7 ciliates (Ci) ml^{-1}. With the exception of the Hfl/Cb pair, the size groups were slightly correlated (Table 3), suggesting that variations in numbers of the different size groups might be linked to trophic relationships or environmental changes.

Fraction 35 to 200 µm (microzooplankton)

The numbers and percentages displayed marked temporal variations (ratio 1:4 over 24 h), but no clear trend was evident (Figs. 3 and 4; Table 4), so that here, again, means could be used.

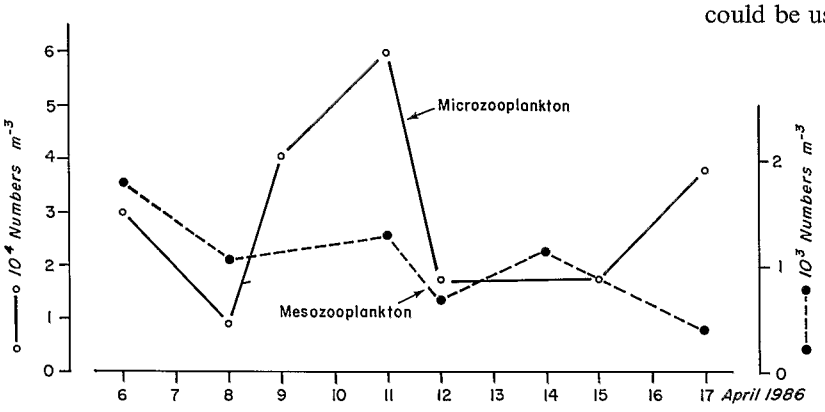

Fig. 3. Abundance of microzooplankton (35 to 200 μm) and mesozooplankton (200 to 2 000 μm) components measured at Station 6 on seven dates in April 1986

Table 4. Microzooplankton abundance (nos. m^{-3}) on 7 d in April 1986 at Station 6 for Size Classes A (35 to 100 μm) and B (100 to 200 μm). Percentages are given in parentheses; –: no data

Microzooplankton components	6 April		8 April		9 April		11 April		12 April		15 April		17 April	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Tintinnids	11 424 (67.75)	3 634 (26.78)	5 150 (76.95)	909 (28.56)	11 163 (75.27)	12 300 (47.14)	13 569 (73.72)	16 680 (41.06)	3 830 (61.04)	1 267 (12.02)	6 510 (54.04)	183 (3.05)	15 943 (68.09)	575 (3.65)
Naked ciliates	475 (2.79)	104 (0.77)	510 (7.62)	85 (2.67)	502 (3.38)	223 (0.85)	732 (3.98)	732 (1.80)	471 (7.5)	289 (2.74)	569 (4.12)	13 (0.65)	489 (2.09)	196 (1.24)
Foraminifers	79 (0.47)	26 (0.19)	66 (0.98)	26 (0.82)	131 (0.88)	13 (0.05)	157 (0.85)	157 (0.39)	–	–	15 (0.12)	–	–	–
Radiolarians	–	–	–	–	–	–	–	–	–	–	19 (0.16)	–	–	13 (0.08)
Naupliar copepods	3 059 (18.14)	7 896 (58.19)	510 (7.62)	1 418 (44.56)	1 608 (10.84)	11 4123 (43.73)	2 474 (14.91)	17 621 (43.37)	1 202 (19.16)	5 929 (56.24)	2 585 (21.46)	2 719 (45.32)	5 485 (23.43)	5 987 (38.01)
Post-naupliar copepods	–	1 281 (9.44)	–	431 (13.55)	–	1 346 (5.16)	26 (0.14)	2 876 (7.08)	–	2 107 (19.98)	117 (0.97)	2 457 (40.96)	57 (0.24)	7 582 (48.13)
Bivalve larvae	1 595 (9.46)	497 (3.66)	366 (5.47)	202 (6.36)	1 321 (8.91)	185 (0.71)	1 020 (5.54)	1 935 (4.76)	550 (8.76)	662 (6.28)	1 725 (14.32)	366 (6.10)	1 036 (4.43)	667 (4.23)
Gastropods	104 (0.62)	79 (0.58)	–	19 (0.60)	13 (0.09)	170 (0.65)	26 (0.14)	157 (0.39)	26 (0.41)	85 (0.81)	431 (3.58)	117 (1.96)	129 (0.55)	183 (1.16)
Eggs	131 (0.77)	53 (0.39)	91 (1.37)	85 (2.67)	53 (0.36)	366 (1.40)	104 (0.57)	471 (1.16)	196 (3.12)	85 (0.81)	75 (0.62)	–	255 (1.09)	91 (0.58)
Annelids	–	–	–	6 (0.19)	–	40 (0.15)	–	–	–	119 (1.13)	–	66 (1.10)	–	66 (0.41)
Larvaceans	–	–	–	–	40 (0.27)	40 (0.15)	26 (0.14)	–	–	–	–	53 (0.87)	14 (0.06)	340 (2.16)
Total	16 867	13 570	6 693	3 181	14 831	26 095	18 407	40 629	6 275	10 543	12 046	5 974	23 412	15 700

Of the total microzooplankton, 43% was in Size Class A (35 to 100 μm) and 57% in Size Class B (100 to 200 μm). Class A mainly consisted of protozoans constituting 73% of the total number (the tintinnids *Rhabdonella* sp., *Codonellopsis* sp. and *Epiplocylis* sp. = 68%; the naked ciliates = 5%). The foraminifers and radiolarians were very poorly represented (<1%). Metazoans accounted for only 27%. The second most abundant taxon consisted of naupliar copepods (18%), and the third of meroplanktonic bivalve larvae (8%). In Class B, protozoans accounted for 33% of the total numbers, 23% being tintinnids. Metazoans were markedly dominant, accounting for 67% of the total. Copepod nauplii were the most abundant organisms (41%). Bivalve larvae were still present, but in numbers not exceeding 7% (Fig. 4B). There was a significant positive correlation (at the 95% confidence level) between the number of tintinnids and the number of copepod nauplii in both size-classes (Table 5), with numbers for these two taxa increasing simultaneously on 9, 11 and 17 April, and decreasing simultaneously on 8, 12, and 15 April.

Table 5. Parameters of regression lines between tintinnids and naupliar copepods for Size Classes A (35 to 100 μm) and B (100 to 200 μm); $N=7$

Size Class	Correlation coefficient	Slope of line	Height of line
A	0.806	2.267	4 313
B	0.820	1.031	−927

Fraction >200 μm (mesozooplankton)

Temporal variations are shown in Figs. 3 and 5 and in Table 6. No significant variations in percentages were observed over the 11 d period, so mean values were used in the calculations. In April 1986, copepods were the dominant taxon, constituting 67% of the total mesozooplankton. Chaetognaths and larvaceans accounted for 5 and 13% of the total, respectively.

Microphagous organisms (copepods, euphausiacean larvae, mysidacean larvae, *Leucifer* sp., ostracods, foraminifers, Thecosomata, gastropods, bivalve larvae and larva-

Table 6. Variations in mesozooplankton abundance (nos. m^{-3}) on 6 d in April 1986 at Station 6. Percentages are given in parentheses; –: no data

Mesozooplankton components	April:					
	6	8	11	12	14	17
Copepods >2 mm	35 (1.99)	71 (6.76)	59 (4.60)	32 (4.41)	82 (6.97)	22 (5.10)
Copepods <2 mm	1 040 (59.02)	616 (58.67)	870 (67.81)	368 (5.76)	715 (60.80)	326 (75.63)
Decapods	15 (0.85)	3 (0.29)	19 (1.48)	37 (5.10)	21 (1.79)	7 (1.62)
Ostracods	4 (0.23)	2 (0.19)	5 (0.40)	3 (0.41)	6 (0.51)	1 (0.23)
Foraminifers	4 (0.23)	2 (0.19)	3 (0.23)	–	–	–
Pteropods (Thecosomata and Gymnosomata)	43 (2.44)	66 (6.29)	43 (3.35)	56 (7.72)	29 (2.47)	7 (1.62)
Gastropod + bivalve larvae	332 (18.84)	48 (4.57)	45 (3.51)	12 (1.66)	23 (1.96)	17 (3.94)
Fish lavae	3 (0.17)	1 (0.09)	2 (0.16)	2 (0.28)	1 (0.09)	1 (0.23)
Plutei	42 (2.38)	–	7 (0.55)	–	–	–
Chaetognaths	79 (4.48)	77 (7.33)	81 (6.31)	40 (5.52)	45 (3.83)	21 (4.87)
Eggs	1 (0.06)	–	1 (0.08)	–	–	1 (0.23)
Larvaceans	159 (9.02)	157 (14.95)	164 (12.08)	170 (23.44)	252 (21.43)	27 (6.26)
Annelids	5 (0.28)	7 (0.66)	4 (0.31)	5 (0.69)	2 (0.17)	1 (0.23)
Total	1 762	1 050	1 283	725	1 176	431

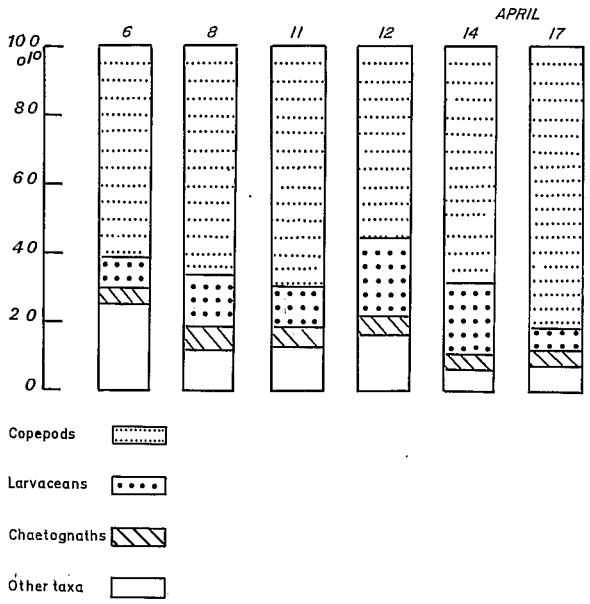

Fig. 5. Relative percentages of mesozooplankton numbers at Station 6 on six dates in April 1986

ceans) made up 83 to 93% of the total. Predators (larvae of certain decapods, amphipods, Gymnosomata, fish larvae, chaetognaths, annelids) accounted for the remainder, i.e., 7 to 17%.

Discussion

In comparative studies of seston components, the main difficulty lies in calculating the ratios C:chlorophyll, C:ATP, and C:vol. We calculated the first and the third ratios, and used values found in the literature for the second.

Conversion of chlorophyll concentrations and mean volumes into carbon

Estimation of phytoplanktonic carbon (CPh) from chlorophyll

A C:chlorophyll value of 50 was calculated for the Tikehau phytoplankton, both experimentally from measurements of ^{14}C incorporation, and in situ in the absence of large-sized grazers (Charpy-Roubaud et al. 1989). This value is identical to that given by Ryther and Yentsch (1957), and lies within the range reported by Takahashi et al. (1985) for picoplankton: 15 to 79 for cyanobacteria and 8 to 77 for microalgae.

Estimation of carbon in the various taxa by mean volume

To assess the relative abundance of the various taxa, we calculated the weight of their carbon content by multiplying their mean number by their mean volume. The mean volume

Table 7. Variations in cell numbers, mean individual volume (Miv), and equivalent spherical diameter (ESD) of cyanobacteria (Cb), phytoplankton other than cyanobacteria (Phy), heterotrophic flagellates (Hfl) and naked ciliates (Ci) over period of 7 d in April 1986. Percentages are given in parentheses

Taxa	Cell nos. (10^6 m^{-3})	Miv (μm^{-3})	ESD (μm)	Biomass (mgC m^{-3})
Cb	151 285±1 677	0.1–2[a]	0.6–1.5[a]	6.05[b] (33.54)
Phy	2 129±15	7 446±6.18	5.23	1.27±1.08 (7.04)
Hfl	71.4±13.80	542±96	10.11	3.10±0.67 (17.18)
Ci	6.68±1.23	14 246±7 427	30.08	7.62±1.40 (42.24)

[a] After (Takahashi et al. 1985)
[b] Calculated using Miv = 0.1 μm^{-3}

per ml thus obtained for each taxon (Table 7) was converted into carbon using conversion factors. For microalgae, heteroflagellates and ciliates, we used 0.08 pg C μm^{-3}, the conversion factor recommanded by a number of authors (Beers and Stewart 1970, Hirota and Szyper 1976, Burkill 1982, Sherr et al. 1984). For cyanobacteria, we used 0.4 pg C μm^{-3} (Takahashi et al. 1985). 59% of the pico- and nanoplankton was made up of heterotrophic organisms (flagellates and ciliates) and 41% of autotrophs (cyanobacteria and microalgae). Heterotrophic bacteria (which had not been counted) were not taken into account, so the biomass of heterotrophic organims was actually greater than 59%.

Comparison of phytoplanktonic carbon values (CPh) obtained from chlorophyll with those obtained from mean volume

The CPh value estimated from chlorophyll (12.5 mg m^{-3}) was nearly double that estimated from mean volume (7.3 mg m^{-3}). This difference may have arisen from overestimation of the C:chlorophyll ratio or from underestimation of the C:vol ratio. As the growth rate of Tikehau phytoplankton is very high (doubling time = 3.5 h; Charpy 1987) the chlorophyll ratio is unlikely to be too high, since a lower ratio would mean even shorter doubling time, which is highly improbable. The discrepancy must therefore be due to an underestimation of the C:vol ratio for cyanobacteria plus algae. We know that all the cyanobacteria (cyano) and 60% of the algae pass through a 3 μm filter. This can be expressed as follows:

$$\text{CPh} < 3\ \mu\text{m} = C_{\text{cyano}} + 0.6\, C_{\text{algae}}\ ; \qquad (2)$$

3 to 35 μm CPh comprises the remaining 40% of the algae, i.e., 3 to 35 μm CPh = 0.508 mg C m^{-3} (1.27 × 0.40). This value is 2.3 times lower than the value estimated from chlorophyll (1.2 mg C m^{-3}), and we can therefore correct

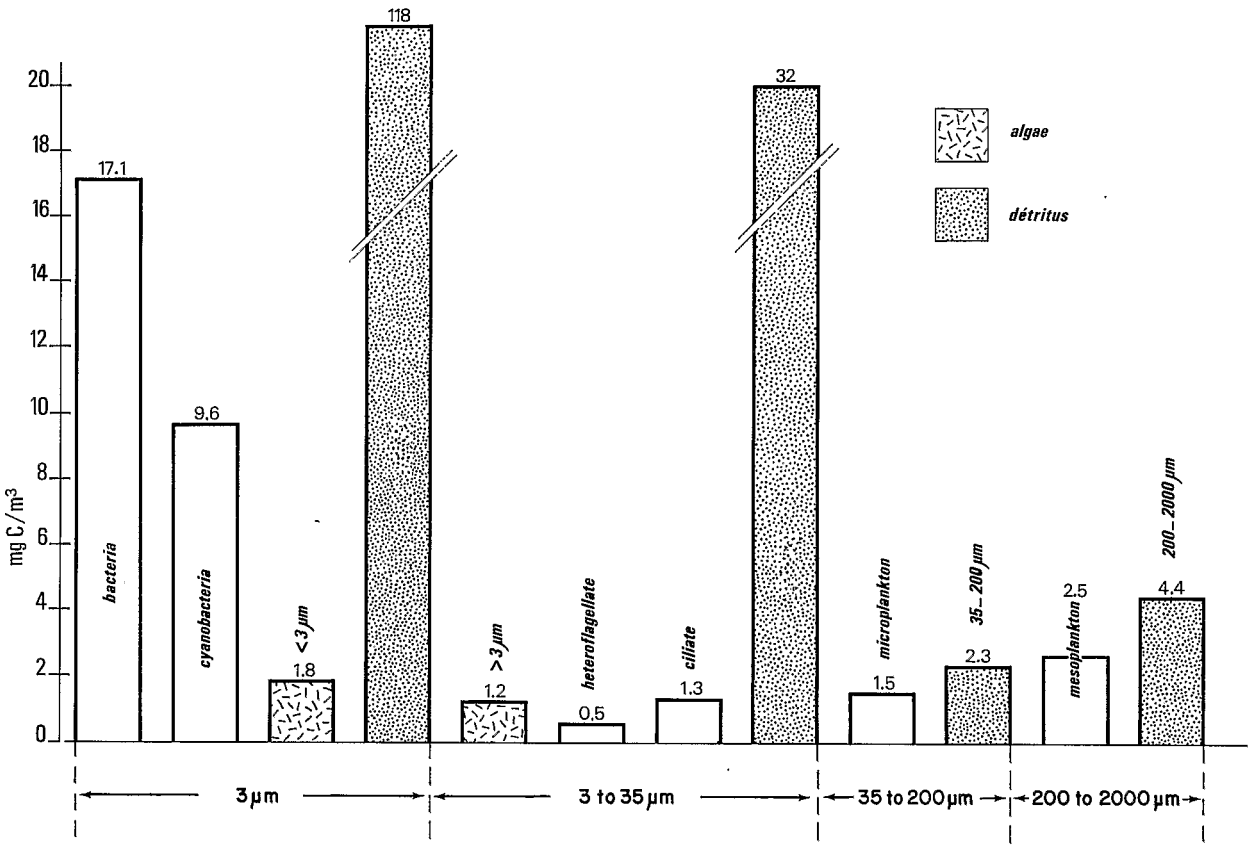

Fig. 6. Size distribution of organic seston weight (mg C m^{-3}) for different size-classes of seston (<3 µm, 3 to 35 µm, 35 to 200 µm, 200 to 2 000 µm)

the carbon value of algae <3 µm by multiplying by 2.3, which gives:

$$\text{CPh} < 3\ \mu\text{m} = C_{\text{cyano}} + 0.6 \cdot 2.3\ C_{\text{algae}} . \quad (3)$$

The value for C_{cyano} now becomes 11.4−1.8 = 9.6 mg m^{-3}; the C:vol values to be used should, therefore, be 0.18 pg C m^{-3} for algae and 0.64 pg C m^{-3} for cyanobacteria.

Estimation of carbon in heterotrophic bacteria (CBh)

As the heterotrophic bacteria are contained in the <3 µm fraction, heterotrophic flagellates and ciliates being >3 µm in size, we can say that:

$$\text{CBh} = \text{LPOC} < 3\ \mu\text{m} - \text{CPh} < 3\ \mu\text{m}$$
$$\text{CBh} = 28.5 - 11.4 = 17.1\ \text{mg m}^{-3}. \quad (4)$$

CBh can be seen to be markedly higher than CPh (17.1 mg m^{-3} vs 12.5 mg m^{-3}).

Living carbon (LPOC) in 3 to 35 µm size-class: comparison of values estimated from ATP with those obtained from mean volumes

The 3 to 35 µm LPOC = CPh 3 to 35 µm + $C_{\text{flagellates}}$ + C_{ciliates} = 1.2 + 3.1 (estimated vol) + 7.6 (estimated vol) = 11.9 mg C m^{-3}. This value is four times higher than the 3 to 35 µm LPOC obtained from ATP (3 mg C m^{-3}). Therefore, the C:vol ratio of the nanozooplankton was overestimated, or our counts included a large proportion of dead organisms despite the fact that we stained nuclei with DAPI before counting. If the LPOC value obtained from ATP is regarded as a good estimate, we have a value of 1.8 mg C m^{-3} for ciliates for nanozooplankton, which can be broken down as follows: 0.5 mg C m^{-3} for heteroflagellates and 1.3 mg C m^{-3} for ciliates.

Summary of carbon estimates for the various taxa

Fig. 6 summarizes the carbon values, and shows that heterotrophs account for 64.5% of the planktonic biomass.

Comparisons with other years and other areas

The high proportion of detritic carbon recorded in the present study was also reported by Charpy (1985) and Charpy et al. (1986), and appears to be general for suspended particles, since Gerber and Marshall (1982) found 77 to 84% of detritic POC at Enewetak atoll, and Winn and Karl (1984) 70 to 90% in ocean waters near the Hawaiian Islands.

The heterotrophic plankton contributed 68.5% of the living carbon and autotrophic plankton 31.5%. The latter's contribution was greater than in previous years, when it ranged from 13 to 25% (Charpy 1985).

Composition of nanoplankton(3 to 35 μm)

The biomass of the heterotrophic nanoplankton was 1.8 mg C m^{-3}, a value similar to that recorded at Kaneohe Bay in Hawaii (2.20 mg C m^{-3}) by Hirota and Szyper (1976) and those obtained for protozoans $<4\,000\ \mu m^{-3}$ on the south-east continental shelf of the United-States (2.5 ± 2.1 mg C m^{-3}; Sherr et al. 1986), and higher than values found in the waters of the Australian Barrier Reef (0.73 ± 0.43 mg C m^{-3}) by Sherr et al.

However, the method used by the above authors to assess nanozooplankton POC differed from ours. Like Beers and Stewart (1970), many authors (Hirota and Szyper 1976, Burkill 1982, Sherr et al. 1986) calculated POC by conversion of volume into carbon, a method that we used to prepare Table 7, but which overestimates living heterotrophic carbon.

Composition of microplankton (35 to 200 μm)

The POC content of microplankton was 1.52 mg C m^{-3}. POM can be estimated using the value suggested by Ryther (1956): POM:POC=2. This gives us 37% POM in the seston, which is higher than values recorded for Californian waters (11 to 23%; Beers and Stewart 1969) and about the middle of the range of values found in the Northern Pacific central gyre (16 to 59%; Beers et al. 1982). Plankton weight constitutes only 16% of the total seston weight.

The combined POC of nano- and microzooplankton was 3.3 mg C m^{-3}, which is low compared with values obtained in Kaneohe Bay (33.5 mg C m^{-3}) by Hirota and Szyper (1976) and in southern California nearshore waters (7.6 to 1 200 mg C m^{-3}) by Beers et al. (1980). It must again be pointed out, however, that the POC assessment method used by these authors, consisting of conversion of volume into carbon, makes it difficult to compare their values with ours.

Distribution of numerical abundance by size-class

While cyanobacteria are widely and abundantly represented in the sea (Johnson and Sieburth 1979), the mean number counted at Tikehau (151 000 ml^{-1}) is one of the highest reported in the literature. It is equalled only in "bloom" periods in nearshore waters of the USA and Japan (Waterbury et al. 1979, Takahashi et al. 1985), or in oceanic areas (Johnson and Sieburth 1979).

The abundance of the <3 μm size-class in the phytoplankton biomass at Tikehau is characteristic of tropical waters (Hirota and Szyper 1976, Herbland and Le Bouteiller 1981, Li et al. 1983, Herbland et al. 1985).

On the other hand, the mean number of heterotrophic flagellates is low in comparison with values found in coastal waters of the USA and in many oceanic areas (Davis and Sieburth 1982, Sherr et al. 1984).

The mean volume of aloricate ciliates is comparable to that of the eastern continental shelf of the USA. Their mean volume (14 000 μm^3) is markedly higher than that reported by Sherr et al. (1986), but similar volumes are not unusual (Rassoulzadegan 1977).

It is difficult to compare our nanoplankton counts with those of authors who used an inverted microscope (Beers and Stewart 1967, 1969, 1971, Hirota and Szyper 1976, Beers et al. 1980, 1982, Revelante and Gilmartin 1983), since the method used by the above authors considerably underestimates numbers compared with epifluorence microscope procedures (Davis and Sieburth 1982).

Our counts of tintinnids and copepod nauplii were five times lower than those obtained in Enewetak lagoon (Gerber and Marshall 1982), but similar to those recorded for copepod nauplii at the Great Barrier Reef (Sammarco and Crenshaw 1984).

The total microzooplankton displayed a one- to six-fold variation over the study period and one- to four-fold variation over 24 h (8 to 9 April). This variability may have resulted from lack of homogeneity or from mass hatching or reproduction with a resultant considerable increase in abundance of the main groups of organisms counted (loricate ciliates, bivalve larvae and copepod nauplii). At 29 °C the generation time of tintinnids is certainly shorter than 24 h. At 18 °C it is 12 h for *Eutintinnus pectinnis* and *Tintinopsis acuminata*, and 24 h for *Heliscostomella subulata* (Heinbokel 1978). At 17 °C it is 6.6 to 13.5 h for *E. lusundae* and 10.0 to 26.9 for *Favella taraikaensis* (Taniguchi and Kawakami 1983). Such short generation times can lead to spectacular increases in abundance during periods when food is plentiful (autotrophic and heterotrophic bacteria). Finally, bivalve and copepod nauplii can greatly increase in numbers as a result of mass hatching. However, the concomitant increase in numbers of all three main taxa suggests that the observed variations were linked to spatial heterogeneity of the microplankton.

The total mesozooplankton displayed a one- to four-fold variation. A trend to decreasing numbers was apparent during our study. The mesozooplankton data were far more homogeneous than those for the microzooplankton. Since the organisms in these two similar size-classes were collected from the same place, at intervals of only a few minutes, inadequate sampling may have distorted the microzooplankton data.

Origin of detritus

Organic detritus in a lagoon can be planktonic (dead organisms and moults) or terrigenous (rare in the Tuamotu atolls), or it can be produced by reef corals. In the case of atolls, the

latter source is by far the most important. On the basis of underwater observations, many authors have reported the presence of mucus aggregates resembling snow-flakes (Johannes 1967, Marshall 1968, Qasim and Sankaranarayanan 1970, Coles and Strathmann 1973). The mucus is not inert over time, but tends to become nitrogen-enriched (Herndl and Velimirov 1986). Finally, algal debris can sometimes be very abundant (Johannes and Gerber 1974).

The food web

In the lagoon, the food web is dependent on several sources: planktonic and benthic primary production, heterotrophic bacteria (dependent in turn on organic detritus), dissolved organic substances, and mucus aggregates whose nutritive value has been demonstrated by Johannes (1967), Ducklow and Mitchell (1979a, b) and Herndl and Velimirov (1986).

Heterotrophic bacteria are ingested mainly by protozoans (Fenchel 1982, Landry et al. 1984, Laval-Peuto et al. 1986, Sherr and Sherr 1987) and, to a lesser extent, by nanoplankton algae (Estep et al. 1986). Cyanobacteria are ingested and digested by protozoans, but persist intact in the gut and fecal pellets of coastal copepods (Johnson et al. 1982). Algae are ingested both by protozoans (Heinbokel 1978) and by metazoans (Capriulo and Carpenter 1980). Protozoans are cannibalistic (Sheldon et al. 1986) and are used as food by the metazoans (Stoecker and Sanders 1985). Detritus is ingested by heterotrophic bacteria, protozoans and copepods (Gerber 1974, Gerber and Marshall 1982, Sherr et al. 1982, Poulet 1983).

The data obtained during this study have enabled us to describe and quantify the various components of the organic seston. Primary production, zooplankton production and the impact of grazing and regeneration of nutrients are the aim of two other papers (Le Borgne et al. 1989, Charpy-Roubaud et al. 1989).

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