

Particulate organic matter fluxes in a Tuamotu atoll lagoon (French Polynesia)

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ABSTRACT: The standing stock and chemical composition of suspended particles ($< 35 \mu\text{m}$) were monitored in the lagoon of Tikehau Atoll from 1983 to 1987 and in surrounding oceanic waters (upper 250 m) during 4 cruises. Trapping rate of particulate material was measured between 1986 and 1987 and net export of particulate organic matter (POM) was roughly estimated using monthly average lagoon POM concentration and monthly average flow of water measured in the passage and the reef-flat spillways. Results showed that deep chlorophyll maxima in oceanic waters could reach 0.24 mg m^{-3} and were observed between 100 and 200 m even when ATP, POC, PON and POP concentrations were higher in the upper 100 m. POM concentration was homogeneous in the lagoon but varied considerably with time especially following 2 hurricanes in 1983. POM concentration was 30 to 40 % higher in samples taken close to the bottom than in the water column. An oceanic station near the atoll was strongly influenced by the lagoonal discharge but POC export from the lagoon to the ocean represents only 6 % of phytoplankton production. The POM content of Tikehau lagoon lies within the range recorded for coral reef areas and is made up of suspended particles 50 % of which are smaller than $5 \mu\text{m}$. Their sedimentation ($350 \text{ mg C m}^{-2} \text{ d}^{-1}$) represents 80 % of phytoplankton production.

INTRODUCTION

Of the 84 atolls of French Polynesia, 76 constitute the Archipelago of Tuamotu. The lagoons of the archipelago play an important role in the French Polynesian economy: cultured pearls from pearl oyster aquacultures in Tuamotu atoll lagoons are French Polynesia's major export; in addition, lagoon fisheries supply a major part of the local fish requirement.

An estimate of lagoonal productivity is necessary to assess the lagoons' potential for exploitation. Such estimates are difficult to make due to the diversity of lagoonal primary producers: phytoplankton, macrophytes, sand microphytes, and epilithic and symbiotic microphytes. Moreover, the flux of detritus particles flowing from the coral reefs into the lagoon may also be important to lagoon organisms (Gerber & Marshall 1982). The particulate organic matter (POM) content of the water column seems to be a good index of lagoon productivity (Charpy 1985). However, so far, only one study has been published on the organic matter found in Polynesian lagoonal waters (Charpy 1985). Other lagoonal studies dealt with phytoplankton productivity (Sournia & Ricard 1975, 1976, Delesalle 1985, Charpy-Roubaud et al. 1989) or phytobenthos productivity (Sournia 1976, Charpy-Roubaud 1988).

Measurements of organic material deposition are very important. Nutrient requirements for lagoonal production may be met through recycling of autochthonous material in the sediments. One of the principal factors which governs rates of nutrient regeneration from sediments is the amount of organic matter incorporated into those sediments from the water above (Koop & Larkum 1987).

Polynesian atolls may be divided into open and closed atolls. The export rate of organic material from an open atoll may be considered as the net production of the atoll. Comparisons between the export of POM and other lagoonal fluxes allows an estimation of the relative importance of lagoonal fluxes and the influence of atoll morphology on lagoonal communities. We studied the abundance, rate of deposition on the lagoon floor and export rate of POM in an open atoll of the Tuamotu archipelago from 1983 to 1987.

STUDY SITE

The atoll chosen for study was Tikehau, situated in the northwest of the Tuamotu Archipelago; its geomorphological characteristics make it suitable model of a mid-size open atoll.

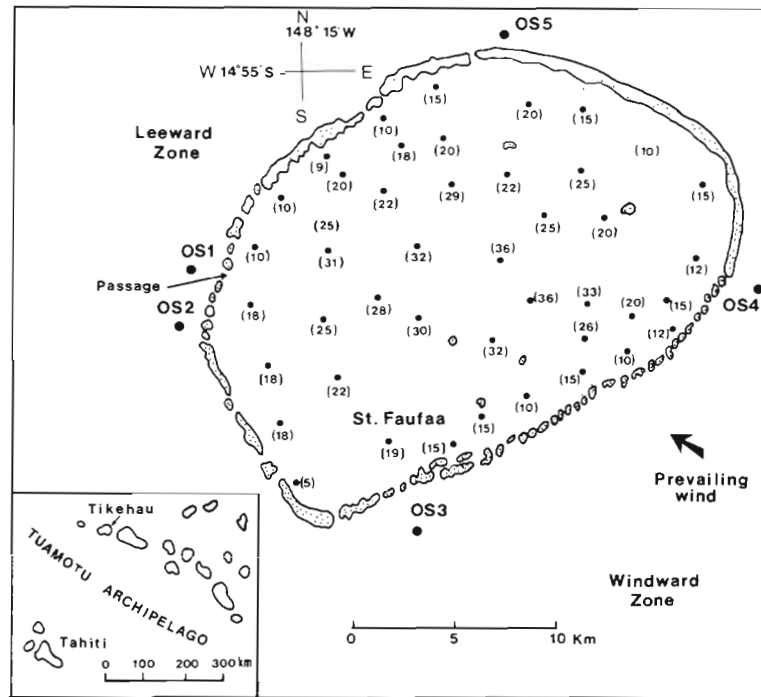


Fig. 1. Location of sampling stations. Ocean Stns OS2 to OS5 were 2 km from Tikehau Atoll and Stn OS1 was located 2 km from the passage between lagoon and ocean. Stn Faufaa served as lagoon reference station. Values in parentheses show depths in metres

Tikehau is almost circular (Fig. 1): its widest diameter (NE-SW axis) is nearly 28 km. The reef rim is ca 78 km long and has a width – taken between the algal ridge and the edge of the lagoon – ranging from less than 300 to 1300 m (Intes 1984). The lagoon has an area of 400 km²; of this 91 % has a depth greater than 15 m, while the average depth is 25 m (Lenhardt 1987). The 25 km² of islands are intersected by reef-flat spillways which link the lagoon and the ocean; one of these forms a 200 m wide and 4 m deep passage at the western end. Except in the passage, currents in spillways generally flow into the lagoon at low speed. The average outward flow in the passage is 700 m³ s⁻¹, therefore a simple average replacement time for waters in the lagoon is 176 d (Lenhardt 1988).

Irradiance is high and 17 % of the light energy measured at the surface reaches 25 m (average depth) (Charpy & Charpy-Roubaud 1990).

Surrounding surface oceanic waters are enriched in nitrogen and phosphorus, probably by vertical turbulent mixing; except for NH₄, mineral nutrient concentrations were lower inside the lagoon than outside (Charpy-Roubaud et al. 1990).

Phytoplankton biomass was low: 0.18 mg chl a m⁻³, dominated by picoplankton; microscopic observations performed during the southern summer showed a high quantity of cyanobacteria (Blanchot et al. 1989). Phyto-

plankton average production (integrated up to 25 m) was 0.44 g C m⁻² d⁻¹ (Charpy-Roubaud et al. 1989).

The zooplankton populations were characterized by successive blooms of copepods, larvaceans, pteropods and salps (Le Borgne et al. 1989). Animals > 200 µm comprised 50 % of the total biomass of all organisms from 35 to 2000 µm. Zooplankton production equalled 34 % of phytoplankton production and its inorganic excretion was respectively 32 and 18 % of phytoplankton nitrogen and phosphorus requirements (Le Borgne et al. 1989).

The lagoon bottom is formed of a fine to very fine calcareous sand. Extensive areas are covered with brown Cyanophyceae. In places, the lagoon bottom is colonised by *Halophila* seagrass beds. Macroalgae are very sparse. Average sand primary production was estimated to 0.25 g C m⁻² d⁻¹ (Charpy-Roubaud 1988).

The upper zone (0 to 2 m) of pinnacles is colonised by algae (*Halimeda*, *Pocockiella*, *Caulerpa*, *Liagora ceranoides*, algal turfs). The windward zone is mainly colonised by large colonies of *Porites lobata* and *Millepora platyphylla* and the leeward zone by *Acropora variabilis*, *A. hyacinthus* and *A. hemprichii*. In the mid zone (2 to 6 m), algae (*Halimeda*, *Caulerpa*) compete with corals (*Montipora*, *Astropora*, *Psammocora*, *Porites*, *Platygyra*, *Pavona*) for sites. The lower zone (6 to 15 m) is occupied by coral patches of *Montipora verru-*

cosa, *Stylocoeniella*, *Platygyra daedalea* and bushes of *Acropora formosa*, *Stylophora pistillata* and *Favia fava*, growing on a detrital or sandy gentle slope (Faure & Laboute 1984, Harmelin-Vivien 1985).

MATERIAL AND METHODS

Station location and sampling strategy.

Ocean: Oceanic waters surrounding the atoll were studied during 4 cruises between 1983 and 1985; the sampling strategy is summarized in Table 1. The 4 stations sampled (OS2 to OS5) are located at 2 km from the reef rim. Samples were taken using 1.7 l Niskin bottles.

Lagoon: Eleven surveys were carried out in the lagoon (Table 2); water was sampled from 10 m depth at 46 stations and in addition at 1 m above the bottom using 5 l Niskin bottles. For each lagoon survey, a station (OS1), located 2 km seawards of the passage from the lagoon to the open ocean, was chosen as a reference for the neighbouring oceanic waters. Pigments and particulate organic carbon and nitrogen (POC and PON) concentrations were also determined in weekly samples collected at the lagoon reference station (Faufaa, 19 m depth) between July 1985 and February 1987.

Chemical analyses of seston. Seawater samples were first prefiltered through a polyamide screen with 35 µm mesh (data on suspended particles larger than 35 µm are presented in another paper: Blanchot et al. 1989). Then, (1) 100 to 300 ml were filtered through a Whatman GF/F filter for pigment analysis; (2) 500 to 1000 ml were filtered through a GF/F processed filter (precombusted for 4 h at 450 °C and precleaned with 1 N HCl) for POC, PON and particulate organic phosphorus (POP) analysis and (3) 250 to 500 ml were filtered through a Millipore 0.45 µm filter for ATP analysis.

Concentrations of chlorophyll *a* (chl *a*) and phaeophytin *a* (phaeo *a*) were determined by fluorescence (Yentsch & Menzel 1963) using a Turner 111 fluorometer.

POC and PON concentrations were determined after rinsing the filter with 20 ml of HCl (0.1 N) with a 185-B Hewlett-Packard CHN analyzer (Gordon & Sutcliffe 1973); a combustion temperature of 720 °C was chosen to reduce carbonate dissociation (Telek & Marshall 1974).

POP was oxidized with persulfate at 110 °C for 1.5 h (Menzel & Corwin 1965) and phosphate concentrations subsequently analysed by spectrophotometry (Strickland & Parsons 1972).

ATP extractions were performed immediately in 5 ml of boiling Tris (0.02 M, pH = 7.85); ATP extracts were

Table 1. Cruises between 1983 and 1985 in oceanic waters near Tikehau Atoll

	July 1983	November 1983	March 1984	November 1985
Name	TIK3	TIK5	TATI	TATU
RV	'Tainui'	'Tainui'	'Coriolis'	'Coriolis'
Stations	OS2, OS5	OS2, OS3, OS4, OS5	OS2, OS3, OS4, OS5	OS2
Depths (m)	0, 25, 50, 100, 150, 200	0, 25, 50, 75, 100, 125, 150, 175, 200, 250	0, 50, 100, 125, 150, 175, 200	0, 25, 50, 75, 100, 125, 150, 200
Parameters measured	Chl <i>a</i> , phaeo <i>a</i>	Chl <i>a</i> , phaeo <i>a</i> , ATP	Chl <i>a</i> , phaeo <i>a</i> , ATP, POP	Chl <i>a</i> , phaeo <i>a</i> , ATP, POP, POC, PON

Table 2. Date and number of stations sampled (n) during 11 surveys in the lagoon of Tikehau Atoll

		1983				1984			1985			
Month	n	Mar	Jul	Sep	Dec	Feb	Nov	Jan	Mar	Apr	Jul	Aug
		21	14	22	17	9	10	7	7	7	7	7

frozen at -20°C until analysis in the Tahiti laboratory. ATP concentrations were measured using the method described by Holm-Hansen & Booth (1966), with a LKB Luminometer and Luciferine-Luciferase preparations from Sigma (FLE 50).

Trapping rate (TR). Fourteen measurements of trapping rate of particulate matter were performed between January 1986 and May 1987, at the Faufaa station. The sediment trap used in this study consisted of a 8 l PVC plastic jar (16×40 cm). The ratio of height to width of the jar was 2.5:1 as recommended by Gardner (1980). No poisoning was done, so as to permit measurements of ATP concentration inside the trap. The jar was mounted 15 m below the surface (4 m above the bottom) on an anchored nylon rope, and supported by a subsurface float 2 m below the surface. Material was collected for 6 to 20 h. Seston was resuspended by magnetic stirring and split into 8 aliquots of 500 ml and 2 of 200 ml. POC, PON, POP, ATP analysis and weight measurements were made in duplicate

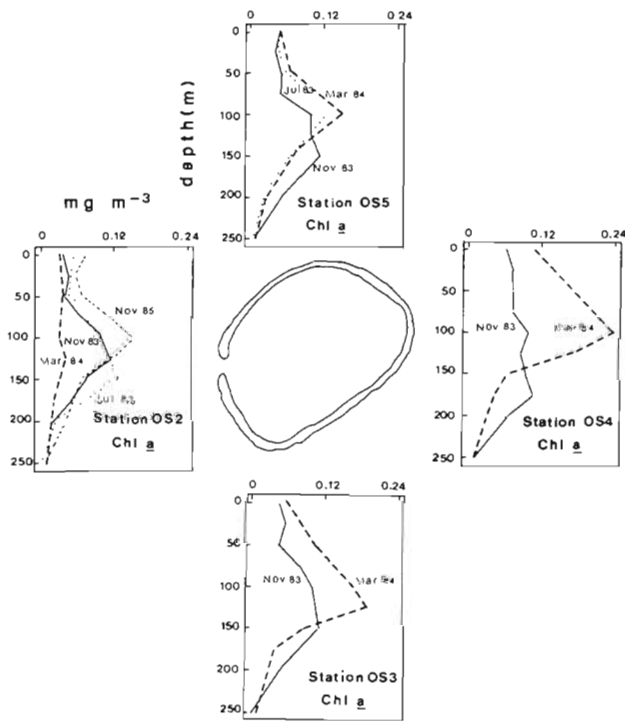


Fig. 2. Chlorophyll a (chl a) concentration profiles (mg m^{-3}) at oceanic stations near Tikehau

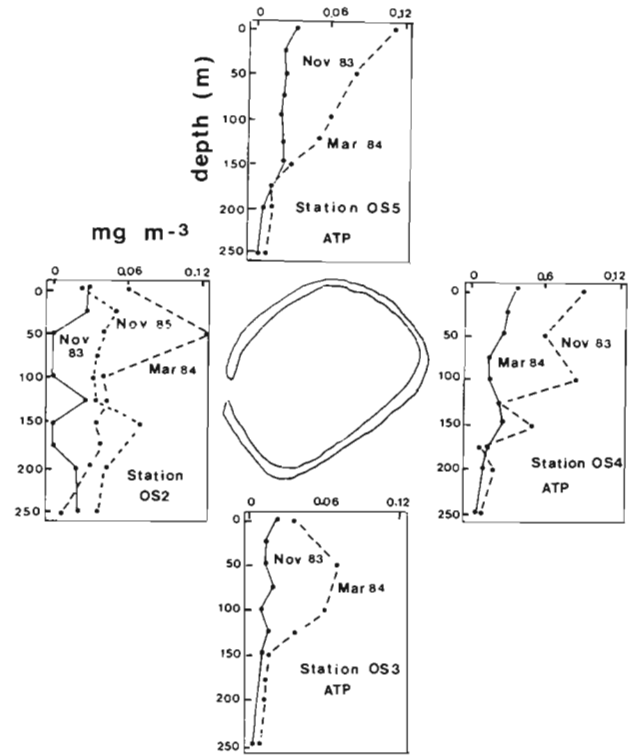


Fig. 3. ATP concentration profiles (mg m^{-3}) at oceanic stations near Tikehau

with the 500 ml aliquots; pigment concentrations were measured on the 200 ml aliquots.

Concentrations of chl a, phaeo a, ATP, POC, PON and POP were measured at 15 m, at the beginning of the experiment.

The trapping rate (TR) was calculated by the equation:

$$TR (\text{mg POM m}^{-2} \text{d}^{-1}) = \frac{(C_T - C_w) \times V}{\Delta t \times S}$$

where C_T = POM concentration in the trap (mg m^{-3}); C_w = POM concentration in the water at 15 m (mg m^{-3}); V = trap volume (m^3); Δt = time interval (d); S = collecting surface area of the trap (m^2).

Assuming that the trapped population of particles is a subset of the suspended population, the settling velocity (SV) can be obtained by the equation:

$$SV (\text{m d}^{-1}) = TR/C_w.$$

RESULTS AND DISCUSSION

POM in oceanic waters

Chlorophyll profiles (Fig. 2) show deep maxima at depths between 100 and 200 m. Concentrations here could reach 0.24 mg m^{-3} in March 1984 (spring) when chl *a* concentrations in the water column were higher than in other months.

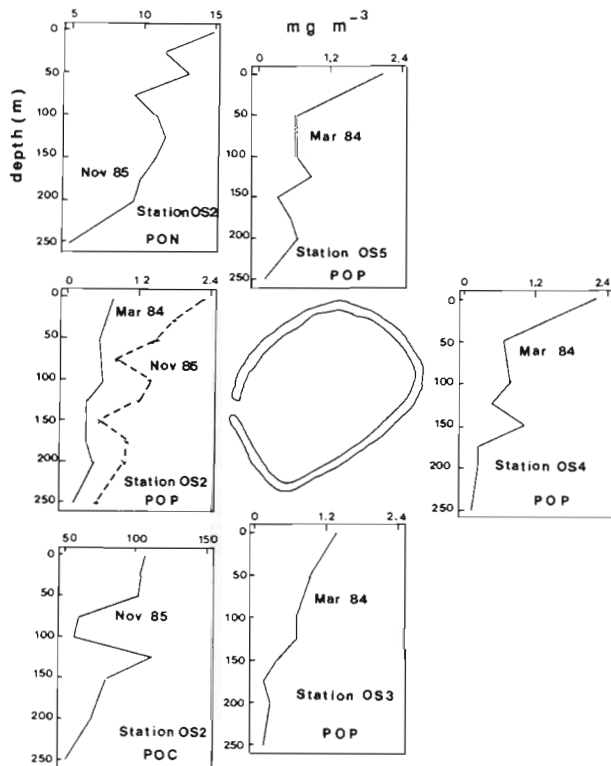


Fig. 4. Particulate organic phosphorus, carbon and nitrogen (POP, POC and PON) concentration profiles (mg m^{-3}) at oceanic stations near Tikehau

ATP concentrations (Fig. 3) were highest in the upper 100 m (0.05 to 0.12 mg m^{-3}) and also higher in March than in November. We did not observe differences between stations.

POP concentrations (Fig. 4) generally decreased with depth. High values observed in surface water at Stns OS4 and OS5 in March 1984 were probably due to detritus export from the reef flat.

All parameters were measured in November 1985 at Stn OS2; however, at that time, this station, located opposite the passage, was influenced by a strong lagoonal water discharge.

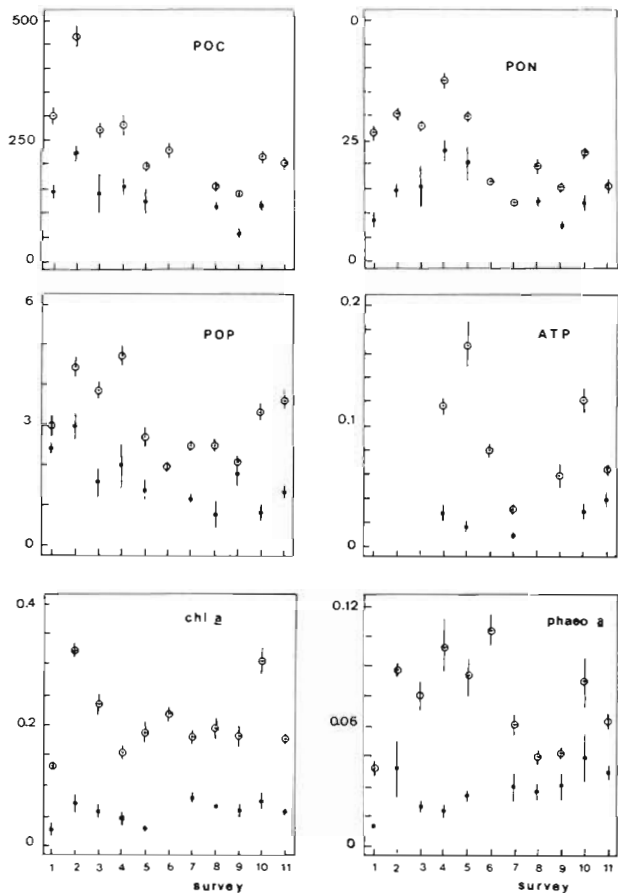


Fig. 5. Mean (\pm SE) POC, PON, POP, ATP and pigment concentrations in lagoon of Tikehau Atoll as a function of survey of sampling \odot : lagoon; \bullet : Stn OS1

POM in the lagoon and at Stn OS1

Survey variability

Average POC, PON, POP, ATP and pigment concentrations in samples taken during the 11 surveys in the lagoon and at Stn OS1 (all stations and depths included) are presented in Fig. 5. The low level of the standard error observed during the surveys demonstrates the relative homogeneity of POM distribution inside the lagoon. Average POC concentration in the lagoon was highest in July 1983 ($466 \pm 23 \text{ mg m}^{-3}$; mean \pm SE). The occurrence of 2 hurricanes (end of March and May 1983) in the western Tuamotu Archipelago is believed to have been responsible for this high POC level. During the other surveys, average POC concentrations were in the range 137 to 301 mg m^{-3} . Average PON concentration was highest in December 1983 ($37 \pm 2 \text{ mg m}^{-3}$) and lowest in August 1985 ($15 \pm 1 \text{ mg m}^{-3}$). Average POP concentration was

highest in July ($4.7 \pm 0.3 \text{ mg m}^{-3}$) and December 1983 ($4.5 \pm 0.3 \text{ mg m}^{-3}$) and lowest in November 1984 ($2 \pm 0.1 \text{ mg m}^{-3}$) and April 1985 ($2.1 \pm 0.2 \text{ mg m}^{-3}$). ATP concentration was measured during 7 surveys and its average was highest in February 1984 ($0.17 \pm 0.019 \text{ mg m}^{-3}$) and lowest in January 1985 ($0.03 \pm 0.003 \text{ mg m}^{-3}$). Average chlorophyll concentration was highest in July 1983 ($0.32 \pm 0.01 \text{ mg m}^{-3}$) and July 1985 ($0.31 \pm 0.01 \text{ mg m}^{-3}$). During the other surveys, the average was in the range 0.13 to 0.23 mg m^{-3} . Average phaeophytin concentration was in the range 0.04 to 0.11 mg m^{-3} .

The level of POM concentration observed at Stn OS1 is correlated with the level of POM concentration observed in lagoonal waters. This is more evident for POC ($r = 0.94$, $p = 0.0005$) and PON ($r = 0.86$, $p = 0.006$) but is also true for chl *a* ($r = 0.59$) and POP ($r = 0.50$). Therefore, the POM water content of Stn OS1 was influenced by the lagoonal discharge. Quasim & Sankaranaryanan (1970) observed a similar feature: POC concentration 2 km from the Karavatti Atoll (Laccadives) was 3 times higher than POC concentration 12 km seawards. We can estimate the average POC and PON concentrations in oceanic waters when the lagoonal discharge is zero by the intercepts of the regression lines: POC concentration at Stn OS1 versus POC concentration in the lagoon ($58 \pm 26 \text{ mg C m}^{-3}$), and PON concentration at Stn OS1 versus PON concentration in the lagoon ($6 \pm 3 \text{ mg N m}^{-3}$). The POP

concentration in oceanic waters can be calculated from the POP average concentration measured in the upper 100 m depths at oceanic stations prospected in March 1984 ($0.7 \pm 0.3 \text{ mg P m}^{-3}$).

Bottom influence

In samples taken near the bottom, we observed an increase of 37 % for POC, 27 % for PON, 31 % for POP, 32 % for chl *a*, 43 % for phaeo *a* and 1 % for ATP (Table 3). The POM increase is probably due to resuspension of detritus. Gerber & Marshall (1982) observed in Enewetak lagoon that particulate carbon and nitrogen were higher in samples collected at 30 to 35 m than at the surface; they suggested that reef detritus settles and accumulates in the deeper water.

Lagoon reference station

Concentrations of POC, PON, POP, ATP and pigments in samples taken in the water column at stations prospected during the surveys (except Faufaa station) were not significantly different (significance level > 0.05) from samples taken in the water column at Faufaa Station (Table 4). Therefore, the Faufaa Station may be considered as a good lagoon reference station. This station was intensively sampled between

Table 3. Comparisons between samples taken in the water column and in the bottom layer. \bar{X} : mean value; DBM: difference between means, %: $\text{DBM} \times 100/\bar{X}$ of the water column; SL: significance level; n: no. of samples

Variable	Water column			Bottom layer			DBM	%	SL
	\bar{X}	\pm SD	n	\bar{X}	\pm SD	n			
POC	208	± 102	391	285	± 149	80	76	37	$< 10^{-3}$
PON	24	± 13	390	21	± 10	80	6.3	27	$< 10^{-3}$
POP	2.9	± 1.4	328	2.7	± 1.6	88	0.9	31	$< 10^{-3}$
ATP	0.09	± 0.06	201	0.09	± 0.06	46	0.001	1	= 0.9
Chl <i>a</i>	0.19	± 0.07	511	0.25	± 0.16	83	0.06	32	$< 10^{-3}$
Phaeo <i>a</i>	0.07	± 0.04	534	0.10	± 0.09	92	0.03	43	$< 10^{-3}$

Table 4. Comparisons between samples taken in the water column at stations studied during the 11 surveys and at Faufaa (1983 to 1985). \bar{X} : mean value; DBM: difference between means, SL: significance level; n: no. of samples

Variable	Survey stations			Faufaa Station			DBM	SL
	\bar{X}	\pm SD	n	\bar{X}	\pm SD	n		
POC	226	± 119	170	202	± 81	85	24	0.09
PON	24	± 12	170	20	± 9	84	4	0.06
POP	2.9	± 1.4	197	2.9	± 1.4	88	0.02	0.92
ATP	0.09	± 0.07	93	0.08	± 0.05	76	0.006	0.54
Chl <i>a</i>	0.19	± 0.06	189	0.22	± 0.11	104	0.03	0.11
Phaeo <i>a</i>	0.06	± 0.04	210	0.07	± 0.04	104	0.003	0.57

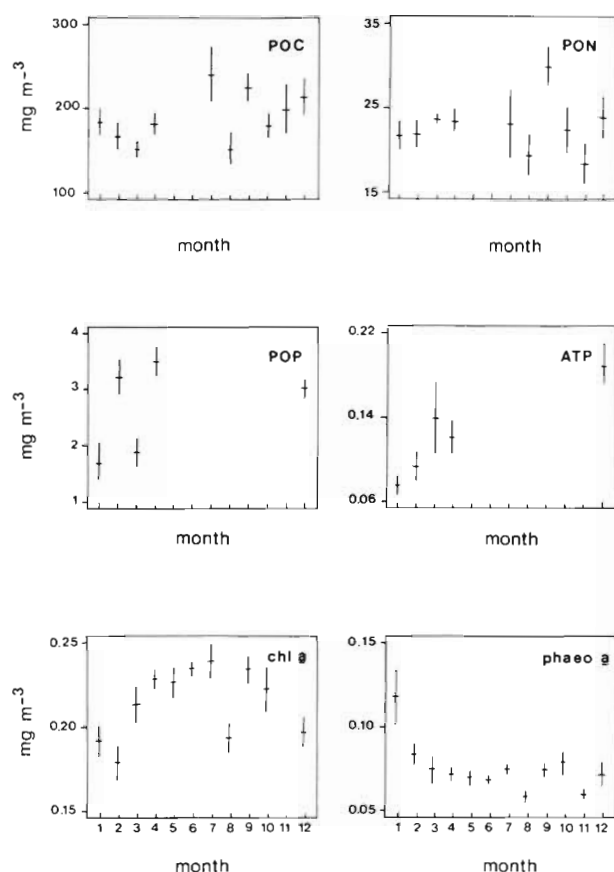


Fig. 6. Mean (\pm SE) POC, PON, POP, ATP and pigment concentrations at Faufaa between November 1985 and February 1987

November 1985 and February 1987 with a view to observing a possible cycle in POM concentration. Monthly average POC concentration (Fig. 6) was in the range 150 to 240 mg C m⁻³, with a maximum in July (southern winter). In Enewetak, Gerber & Marshall (1982) observed that detritus concentration was lower in winter than in summer and they thought that it may

be due to difference in residence time of the lagoon waters (200 d in summer and 20 to 30 d in winter). In Tikehau, lagoonal water residence time was higher in summer (230 d) than in winter (100 d) (Lenhardt 1988); therefore, differences in residence time of Tikehau lagoonal waters were not responsible for differences in POC concentration.

Comparison with other atoll lagoons

To enable comparison of POM content for Tikehau lagoon water, we average 1984 to 1987 data obtained in the water column: POC = 192 \pm 5, PON = 21 \pm 1 and POP = 2.7 \pm 0.1. Apparently there is no relation between residence time of waters in atoll lagoons and their POM content (Table 5). Absolute values of POM concentrations are very different; the variability in measurements of fluxes reflect not only natural variability in these parameters, but also major errors associated with the methods employed (Hatcher 1983).

POM export from lagoon to ocean

Exports (*Ex*) of POC, PON and POP from the lagoon to the ocean can be calculated by the equation:

$$Ex \text{ (mg m}^{-2} \text{ d}^{-1}) = \frac{F \times C_L}{L_s}$$

where F (m³ d⁻¹) = monthly average flow through the lagoon passage and the reef-flat spillways (given by Lenhardt 1988); L_s = lagoon surface area (= 4 \times 10⁸ m²); and C_L = monthly average concentration of POC, PON or POP in the lagoon. Results appear in Table 6. Compared with other lagoonal carbon fluxes, the average POC export (26.3 mg C m⁻² d⁻¹) was low: 6% of the phytoplankton production (440 mg C m⁻² d⁻¹) given by Charpy-Roubaud et al. (1989) and 8% of the

Table 5. Particulate organic carbon (POC; mg C m⁻³) in coral reef lagoon waters. RT: residence time in days. Taken in part from Hatcher (1983) and Marshall et al. (1975)

Lagoon	RT	POC		Source
		Lagoon	Ocean	
Tikehau Atoll	176	192	52	This study
Enewetak Atoll	20–200	20–50	18–30	Gerber & Marshall (1982)
Fanning Atoll	30	80		Gordon (1971), Smith & Pesret (1974)
Canton Atoll	50–95	160 ^a		Smith & Jokiel (1975a, b)
Kavarati Atoll		355	75	Quasim & Sankaranarayanan (1970)
Houtman Atoll		1560–3660	14–42	Hatcher (1983)
South Caicos		130	40	Marshall et al. (1975)
Kanohe Bay		420		Coles & Strathman (1973)
Lizard Island		82–116	185–243	Moriarty (1979)

^a Value derived by chl *a* \times 200

Table 6. Monthly average flow through the lagoon passage and the reef-flat spillways (F ; $m^3 \times 10^{-6} d^{-1}$) calculated from Lenhardt (1988), and export (Ex ; $mg m^{-2} d^{-1}$) of POC, PON and POP from the lagoon to the ocean between 1985 and 1987

Date	F	Ex		
		POC	PON	POP
Mar 1985	43.2	16.7	2.1	0.27
Apr 1985	60.5	20.7	2.3	0.32
Jul 1985	86.4	46.4	4.8	0.72
Sep 1985	77.8	43.8	5.8	–
Oct 1985	60.5	32.7	4.7	–
Jan 1986	34.6	17.5	2.0	0.15
Oct 1986	60.5	22.1	2.1	–
Nov 1986	60.5	30.1	2.7	–
Jan 1987	38.9	13.4	1.7	–
Feb 1987	34.6	20.0	2.5	–
Average:	55.8	26.3	3.1	0.37

ingestion by the zooplankton ($314 mg C m^{-2} d^{-1}$) measured by Le Borgne et al. (1989). In Canton Atoll, Smith & Jokiel (1975b) observed a POC export of 6 to 20 $mg C m^{-2} d^{-1}$ which represented 0.1 to 0.3 % of the lagoonal gross organic carbon production ($6 g C m^{-2} d^{-1}$). These export rates are quite similar in spite of different residence time (50 d in Canton and 176 d in Tikehau) and different lagoonal primary productions ($6 g C m^{-2} d^{-1}$ in Canton and $0.7 g C m^{-2} d^{-1}$ in Tikehau).

POM size and composition

To measure the size structure of suspended particles, water samples were successively filtered through a polyamide net with a 35 μm size mesh, through a 5 μm filter (Millipore), then through a 1.2 μm filter (Millipore) and finally through a GF/F (Whatman) filter. A significant part of the POM was in the 0.4 to 1.2 μm size class (1 to 48 % of the ATP, 36 to 65 % of the POP, 33 to 52 % of the POC and 18 to 22 % of the PON) (Table 7). The results of 7 filtering experiments performed in 1984,

1985 and 1986 with 35 μm mesh size (polyamide net) and then 5 μm and 3 μm pore size (Nuclepore filters) (Table 8) indicate that about 50 % of the POM is constituted of particles smaller than 5 μm , regardless of the variable considered.

The size composition of POM was studied in April 1986: particles < 3 μm accounted for 81 % of the POC and detritus comprised 82 % of the total POM. Phytoplankton accounted for 35 % of the living carbon with a strong dominance of cyanobacteria; heteroflagellates and ciliates accounted for 6 % of the living C (Blanchot et al. 1989).

Sedimentation of particles

The sediment trap was placed at a depth thought to be far enough from the bottom (5 m) to collect only material sinking from the surface layer. Current speeds below 5 m depth in the lagoon are generally lower than $5 cm s^{-1}$ (Lenhardt 1988). Therefore, we assume that resuspension rate = 0 and that the trapping efficiency was maximum. So sedimentation rate (SR) = trapping rate (TR). Results appear in Table 9.

The vertical flux of POC lies within the range of the sedimentation rate expected for coastal waters (Mann 1982). The SR s of carbon and nitrogen (350 and $36 mg m^{-2} d^{-1}$) are close to the values given by Taguchi (1982) for Kaneohe Bay (Hawaii); however, these values are 4 times lower than the values given by Koop & Larkum (1987) for organic C and N deposition in the lagoon of One Tree Island (Great Barrier Reef) and 2.4 times lower than the POC deposition rate given by Chardy & Clavier (1989) for the southwest lagoon of New Caledonia ($844 mg C m^{-2} d^{-1}$). There is a great difference between the deposition rate calculated, for the Canton lagoon, by Smith & Jokiel (1975b): $10 mg C m^{-2} d^{-1}$ and our data; however, they used for their calculation a percentage of organic carbon in suspended material equal to that observed in sediments (0.8 %) even when this percentage was equal to 9 % in

Table 7. Relative abundance of POM among the 3 size fractions (μm) at Faufaa on 23 November (0 and 10 m) and 24 November 1984, (0, 2, 10 and 15 m)

Depth (m)	ATP (%)			POP (%)			POC (%)			PON (%)		
	<1.2	2–5	5–35	<1.2	2–5	5–35	<1.2	2–5	5–35	<1.2	2–5	5–35
0	15	30	55	65	29	6	35	0	65	18	6	76
10	48	0	52	36	20	44	33	1	65	20	5	75
0	29	45	26	65	–	–	52	25	23	27	27	46
2	1	17	82	–	–	–	–	–	–	–	–	–
10	11	14	75	–	–	–	–	–	–	–	–	–
15	3	26	71	65	24	12	34	25	41	22	44	34

Table 8. Means (\pm SE) of POM passing through a 5 μm (1984 and 1985) or 3 μm (1986) pore filter as a percentage of total POM at Faufaa. Standard errors of samples taken at the same date are given

Date	Depth (m)	Chl <i>a</i> (%)	Phaeo <i>a</i> (%)	ATP (%)	POC (%)	PON (%)	POP (%)
23 Nov 1984	0, 10	–	–	47 \pm 2	35 \pm 0	24 \pm 1	75 \pm 19
24 Nov 1984	0, 2, 10, 15	66 \pm 5	–	48 \pm 26	61 \pm 7	57 \pm 3	88
2 Apr 1985	0, 5, 10, 15, 19	57 \pm 25	40 \pm 35	–	43 \pm 14	55 \pm 23	27 \pm 7
9 Apr 1985	0, 5, 10, 15, 19	32 \pm 6	29 \pm 17	68 \pm 11	33 \pm 11	46 \pm 16	47 \pm 20
12 Jul 1985	0	57	34	30	35	32	29
13 Aug 1985	0, 2, 4, 6, 8, 10, 15	25 \pm 4	–	20 \pm 5	–	–	24 \pm 12
7 Apr 1986	0, 5, 10, 19	92 \pm 5	74 \pm 3	75 \pm 24	81 \pm 1	77 \pm 13	99 \pm 2
Average \pm SE		50 \pm 6	45 \pm 8	46 \pm 6	50 \pm 6	54 \pm 5	49 \pm 6

suspended matter (0.7 to 35 μm) of Tikehau lagoon (Blanchot et al. 1989).

The mean sedimentation rate of total pigments: 0.23 $\text{mg m}^{-2} \text{d}^{-1}$ is 4 times lower than the *SR* given by Taguchi (1982) in Kaneohe Bay (Hawaii) and 4 times lower than the chl *a* deposition rate calculated from Charpy & Clavier (1989) in New Caledonia.

The settling velocity of chl *a* (0.6 cm d^{-1}) is comparable to that of the nanoplankton measured in the Hawaiian waters (Takahashi & Bienfang 1983); but it is only half the phaeo *a* settling velocity. In general, phaeo *a* in suspended particles has been attributed to microzooplankton grazing (SooHoo & Kiefer 1982), while that in sinking material caught in sediment traps has been attributed to macrozooplankton grazing (e.g. Lorenzen et al. 1983).

The average POC:PON:POP ratio (mass) in the trapped material was 117:12:1 (i.e. C:N:P = 302:27:1, molar basis); in suspended material, during the time of trapping experiments, the POC:PON:POP ratio (mass) was 68:7:1 (i.e. C:N:P = 176:17:1, molar basis). The trapped material had the same ratio C:N (9.8) as the suspended particles (10) but its C:P ratio (117) was higher than the C:P ratio (68) in suspended particles. The loss of phosphorus in the trapped material indicates that the organic matter was dead; this is confirmed by ATP measurements in trapping material which were all zero.

However, *TR* measurements were performed on 14 occasions at only one station and one depth; therefore, average sedimentation rates are perhaps not representative of lagoon POM sedimentation. Nonetheless, we

Table 9. Trapping rate (*TR*; $\text{mg m}^{-2} \text{d}^{-1}$), settling velocities (*SV*; m d^{-1}) and C:N:P ratio (w/w) of trapped material measured at Faufaa. CV: coefficient of variation (%)

Date	Chl <i>a</i>		Phaeo <i>a</i>		POP		POC		PON		C:N:P
	<i>TR</i>	<i>VS</i>	<i>TR</i>	<i>VS</i>	<i>TR</i>	<i>VS</i>	<i>TR</i>	<i>VS</i>	<i>TR</i>	<i>VS</i>	
7 Jan 1986	0.09	0.6	0.14	1.2	3.6	2.0	254	1.4	19	1.0	71: 5:1
8 Jan 1986	0.07	0.5	0.14	1.2	5.0	2.7	456	2.6	58	3.2	91:12:1
12 Jan 1986	0.06	0.4	0.05	0.6	7.2	6.6	941	8.2	79	5.4	131:11:1
16 Jan 1986	0.24	1.7	0.08	0.7	7.9	3.3	1032	9.0	113	7.5	131:14:1
25 Jan 1986	0.06	0.5	0.06	1.3	0.7	0.1	266	1.7	22	1.2	380:31:1
17 Dec 1986	0.21	1.2	0.11	2.7	3.8	1.2	130	1.0	12	0.9	34: 3:1
18 Dec 1986	0.15	0.6	0.14	2.3	3.4	1.1	122	1.2	12	1.0	36: 4:1
20 Dec 1986	0.15	0.8	0.19	3.9	6.2	3.0	146	0.6	14	0.6	24: 2:1
22 Dec 1986	0.14	0.6	0.13	1.7	4.6	1.5	221	1.4	24	1.8	48: 5:1
9 Feb 1987	0.18	0.6	0.31	0.2	2.4	1.7	–	–	–	–	–
10 Feb 1987	0.19	0.7	0.22	2.0	1.4	1.2	–	–	–	–	–
12 Feb 1987	0.20	0.8	0.26	2.4	1.4	1.2	–	–	–	–	–
26 May 1987	0.05	0.3	0.08	1.4	0.5	0.2	–	–	–	–	–
27 May 1987	0.00	0.0	0.00	0.0	0.5	0.1	–	–	–	–	–
14 Jul 1987	0.03	0.1	0.11	1.1	1.2	0.7	108	0.7	12	0.6	90:10:1
17 Jul 1987	0.01	0.1	0.01	0.1	0.7	0.1	175	0.9	22	0.8	250:31:1
Average	0.11	0.6	0.12	1.4	3.2	1.7	350	2.6	36	2.2	117:12:1
CV	66	72	67	74	78	25	94	116	97	104	

can roughly compare the sedimentation rate with other fluxes measured in the lagoon: POC average *SR* was in the same order of magnitude as phytoplankton production (Charpy-Roubaud et al. 1989) and zooplankton ingestion (Le Borgne et al. 1989), 1.4 times higher than the sandy microphyte production (Charpy-Roubaud 1988) and 13 times higher than the POC export calculated previously. For comparison, in Kaneohe Bay, Taguchi (1982) observed that the carbon sedimentation rate was equal to 42.5% of the phytoplankton production and to 7 times the POC export. In Canton Atoll lagoon, Smith & Jokiel (1975b) calculated that the organic carbon deposition represented 0.2% of the gross lagoon production and between 2 and 0.5 times the POC export. In the southwest lagoon of New Caledonia, Chardy & Clavier (1989) observed that benthic microflora production represented 21% of the input of organic carbon to the bottom.

Given this deposition of organic material in the lagoon, one would expect to find sediments with relatively high organic content. However, levels of organic material in coral-reef sediments are generally low, about 0.5% of dry weight (Vaugelas 1982, Thomassin & Cauwet 1985); this implies that organic material is rapidly consumed and/or remineralized (Hatcher 1983).

Origin of lagoon POM

Charpy & Charpy-Roubaud (1990b) have shown that the detritus reef flat export towards the lagoon is insignificant and the detritus pool (84% of the POC) originates from lagoonal primary production. The phytoplanktonic production ingested and then excreted as fecal pellets by the zooplankton cannot alone explain the level of the POC sedimentation rate: export of POM from the lagoon pinnacles may be the other POC source.

Observed variations in POM content of lagoonal waters are probably not due to variation in primary production. Indeed, maximum POC concentrations were observed in winter when light energy was minimum. Storms are probably responsible for the increase in POM by removing organic matter from the pinnacles. On the other hand, grazing may have a significant effect on POM concentration: in April 1985, 30% of the POC content of lagoonal waters was ingested in 1 wk during a bloom of *Thalia democratica* (Charpy et al. 1986).

CONCLUSIONS

The oceanic waters around the Tikehau atoll are enriched in POM by reef-flat detritus production and lagoonal discharge.

POM content of lagoonal waters is homogeneous in space but shows variations greater than 100% with time, probably due to resuspension during storms.

Average lagoonal POC concentration observed in Tikehau lies within the wide range of data recorded in other coral reef areas. There is no relation between residence time of oceanic waters in the lagoons and lagoonal POC content.

The POM is made up of small particles (50% are < 5 μm); this probably influences the composition of detritivores.

The sedimentation rate represents 80% of the phytoplankton production. The loss of phosphorus during sedimentation indicates that a non-negligible part of the organic matter is mineralized in the water column.

POM export represents only a small percentage of other lagoonal fluxes; therefore, the geomorphology of atolls (closed or open) probably has a light effect on the POM content of lagoonal waters.

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This article was submitted to the editor

Manuscript first received: February 7, 1990

Revised version accepted: January 3, 1991