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Trophic Structure and Productivity of the lagoonal communities of Tikehau atoll (Tuamotu Archipelago, French Polynesia)

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Abstract

Carbon standing stocks and fluxes were studied in the lagoon of Tikehau atoll (Tuamotu archipelago, French Polynesia), from 1983 to 1988.

The average POC concentration (0.7–2000 μm) was 203 mg C m^{-3}. The suspended living carbon (31.6 mg C m^{-3}) was made up of bacteria (53%), phytoplankton <5 μm (14.2%), phytoplankton >5 μm (14.2%), nanozooplankton 5–35 μm (5.7%), microzooplankton 35–200 μm (4.7%) and mesozooplankton 200–2000 μm (7.9%). The microphytobenthos biomass was 480 mg C m^{-2}.

Suspended detritus (84.4% of the total POC) did not originate from the reef flat but from lagoonal primary productions. Their sedimentation exceeded phytobenthos production.

It was estimated that 50% of bacterial biomass was adsorbed on particles. the bacterial biomass dominance was explained by the utilisation of 1) DOC excreted by phytoplankton (44–175 mg C m^{-2} day^{-1}) and zooplankton (50 mg C m^{-2} day^{-1}) 2) organic compounds produced by solar-induced photochemical reactions 3) coral mucus.

50% of the phytoplankton biomass belongs to the <5 μm fraction. This production (440 mg C m^{-2} day^{-1}) exceeded phytobenthos production (250 mg C m^{-2} day^{-1}) when the whole lagoon was considered.

The zooplankton >35 μm ingested 315 mg C m^{-2} day^{-1}, made up of phytoplankton, nanozooplankton and detritus. Its production was 132 mg C m^{-2} day^{-1}.

Introduction

Recent upward revisions in estimates of biomass per bacterium indicate that many earlier biomass values may have to be almost doubled and that bacteria are major components of marine systems

stratified, oligotrophic water column may give rise to dominance of small phytoplankters, relatively high DOM-production rates and a long 'microbial loop' type of food chain (Kiørboe *et al.*, 1990).

Polynesian atoll lagoons are located in oligotrophic waters and dominance of small phytobenthic production represented 55% of the phytoplanktonic production of the Tikehau lagoon.

The aim of this paper was to investigate the activities of lagoonal primary producers (phytoplankton and phytobenthos), zooplankton (nano, micro and mesoplankton) and bacteria.

All data used in this study were obtained during the ATOLL program of the Tahiti ORSTOM Center.

Description of site studied

The atoll chosen as a study site was Tikehau, situated in the north west of Tuamotu archipelago (Fig. 1); its characteristics make it a suitable model of a mid-sized open atoll. A preliminary description of this atoll was given by Harmelin-Vivien (1985). Tikehau is almost circular: its widest diameter is nearly 28 km. The surface of the lagoon is 400 km^2, 91% of the lagoon bottom is deeper than 15 m and the average depth is 25 m (Lenhardt, 1987). Oceanic water enters by the east and south east reef-flat spillways, and exits after a mean residence time of 176 days by the passage located to the west (Lenhardt, 1988).

Material and methods

Suspended material (0.5–35 μm)

Standing stocks: eleven surveys were made in the lagoon between 1983 and 1985 (Table 1); sam-

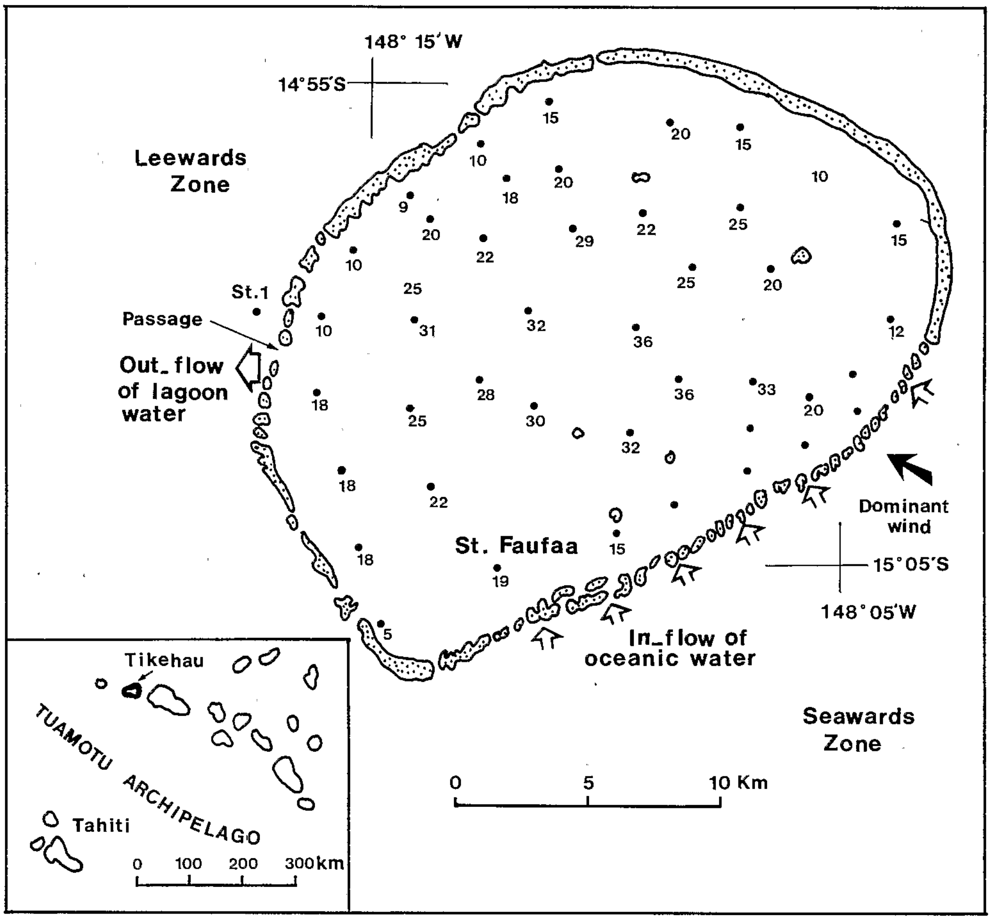


Fig. 1. The atoll of Tikehau: location and depth of sampling stations.

pling was performed at 46 stations, every 10 m

Conversion factors: The living carbon (liv C) the equation:

$$\text{Export (mg C m}^{-2}\text{ day}^{-1}) = F \cdot POC_L / S_L$$

F = annual average flow through the passage and the reef flat spillways; it was estimated as $6 \cdot 10^7$ m^3 day^{-1} by Lenhardt (1988).
POC_L = average POC concentration in the lagoon (mg C m^{-3}).
S_L = lagoon area = 4 10^8 m^2.

The zooplankton (35 μm–2000 μm)

The standing stocks and taxonomic composition of the zooplankton were monitored in the lagoon of Tikehau between April 1985 and April 1986. Microzooplankton (35–200 μm) and mesozooplankton (200–2000 μm) were collected by vertical hauls from the bottom to the surface. These data were supplemented by two 10 day studies of the variability, structure and functioning of the pelagic ecosystem. Excretion and respiration rates were determined from incubation experiments. Using the C:N:P ratio method, net growth efficiencies (K_2) were calculated for the zooplankton. Combined with nitrogen and phosphorus excretion rates, K_2 values enabled the assessment of production rates. Ingestion by animals > 35 μm was calculated by means of assimilation efficiencies. These methods are described in Le Borgne *et al.* (1989).

Microphytobenthic carbon at the sediment water interface

Microphytobenthos biomass and production were studied between 1985 and 1987 (Charpy-Roubaud, 1988):

- microphytobenthos biomass was estimated by sediment chl · *a* concentration measurements
- phytobenthic production was determined by O_2 budgets, measured within clear and dark plexiglass domes. The production of O_2 (BP_{O_2}) may be converted into the gross production of carbon (BP) by the equation:

$$Bp = (BP_{O_2} \cdot 0.375 \cdot PQ) + (R \cdot 0.375 \cdot RQ)$$

R = Respiration during daytime; PQ and RQ = photosynthetic and respiratory coefficients.

Results

Particulate organic matter

POC concentration values (N = 522) ranged from 82 to 893 mg C m^{-3}. The yearly average was significantly ($P < 0.05$) higher in 1983 than in other years (Fig. 2). The occurrence of two hurricanes in March and May 1983 in the Western Tuamotu Archipelago is believed to be responsible for this high POC level. Monthly averages (all years included), presented wide variations but the station location had no influence on POC concentration. The POC concentrations were 40% higher in samples taken near the bottom than in the water column.

Chl · *a* concentration values (Fig. 2) ranged (N = 782) from 0.02 to 1.01 mg m^{-3}. Yearly averages were not significantly ($P > 0.05$) different but monthly averages differed significantly ($P < 0.05$). Chl · *a* concentrations were 37% higher close to the bottom than in the water column.

ATP concentrations (Fig. 2) were lower in 1985 than in other years. Monthly averages differed significantly ($P < 0.05$); ATP concentration was independent of the proximity to the bottom.

Therefore, in order to estimate the lagoonal POM averages, we consider neither 1983 data nor

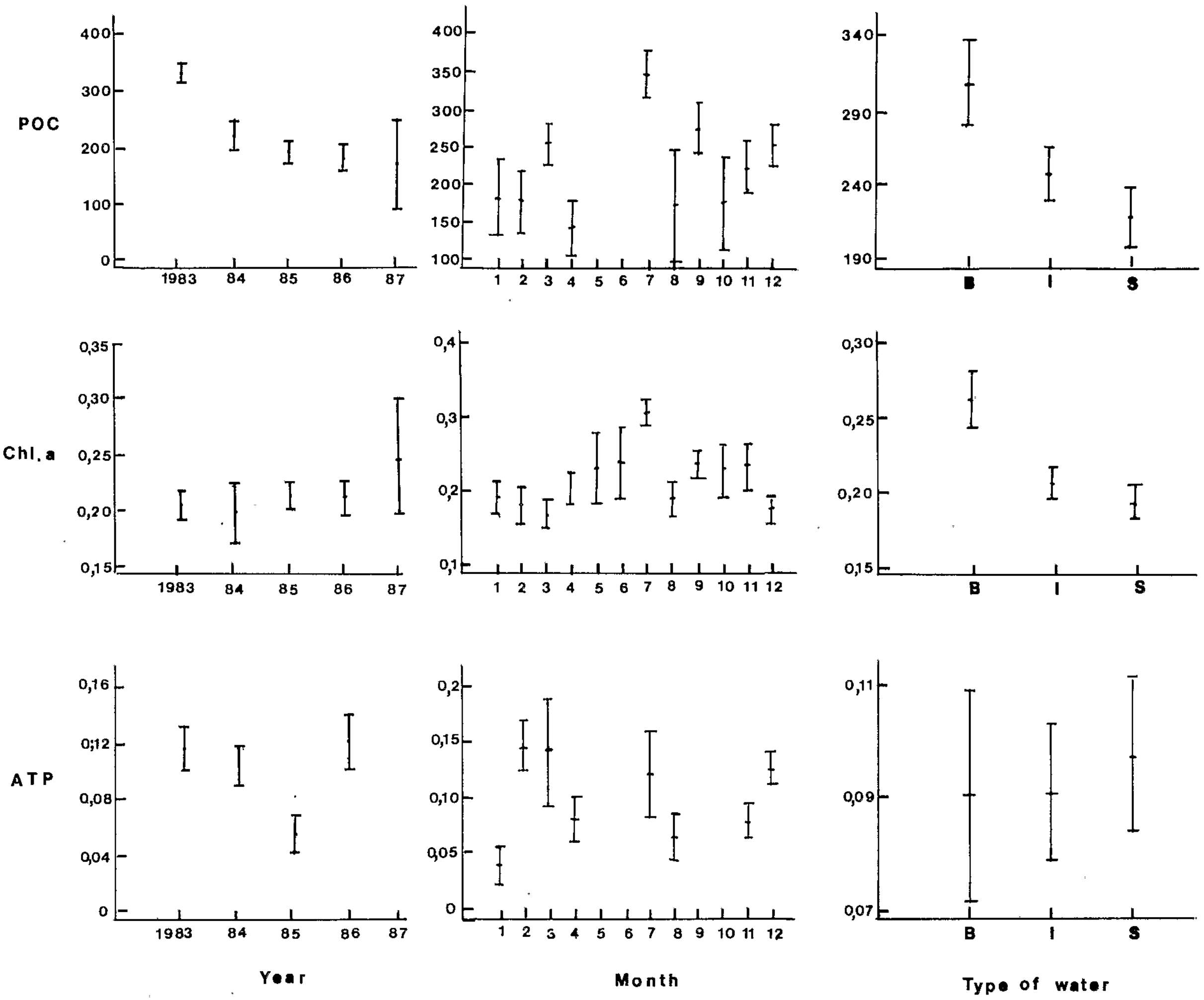


Fig. 2. Means and confidence intervals ($P = 95\%$) for factors 'year', 'month' and 'type of water'; B = samples taken at 1 m above the bottom, I = samples taken between 2 m and the bottom, S = samples taken between 0 m and 2 m.

POM_i = POM average on month i.
N_i = number of months prospected.

The weighted averages and confidence intervals are summarized in Table 2.

The results of seven filtering experiments performed in 1984, 1985 and 1986 with 35 μm mesh size (polyamide net) and then 5 μm pore size (Nuclepore filters) appear in Table 2.

The average sedimentation rates are summarized in Table 2.

The POC export was calculated at 29 mg m^{-2} day^{-1}.

Table 2. Weighted averages and confidence intervals ($P = 95\%$) of chl·*a*, ATP and POC concentration (mg m^{-3}); percentages of particles passing through 5 μm (% < 5 μm) and averages sedimentation rates (SR: mg m^{-2} day^{-1}).

	chl·*a*	ATP	POC
Average	0.18 ± 0.01	0.11 ± 0.01	192 ± 10
N	409	162	290
% < 5 μm	50 ± 11	50 ± 11	46 ± 11
N	27	23	21
SR	0.11 ± 0.06	0	350 ± 218
N	11	11	11

Table 3. Phytoplankton, zooplankton and phytobenthos biomass and fluxes measured in the lagoon of Tikehau. Data from Charpy-Roubaud (1988), Charpy-Roubaud *et al.* (1988), Le Borgne *et al.* (1989), Blanchot *et al.* (1989). B = biomass (mg C m^{-3}); A = assimilation, I = ingestion, P = production (A, I, P = mg C m^{-3} day^{-1}); E = Excretion of organic P (mg P m^{-3} day^{-1}).

Organism	B	A	I	P	E	Ratios
Phytoplankton						
<5 μm	4.5					
>5 μm	4.5					
Total	9.0	17.6		?	?	C/chl · a = 50
Zooplankton						
<35 μm	1.8		?	?	?	
Zooplankton						
35– 200 μm	1.5		2.6	1.2	8.4	
200–2000 μm	2.5		10.0	4.1	19.2	
Total	4.0		12.0	5.3	27.6	C/P = 52
Detritus						
35– 200 μm	2.3					
200–2000 μm	4.4					
Total	6.7					
Phytobenthos	B (mg chl · a m^{-2})			P (mg C m^{-2} day^{-1})		
	9.6			250		

Plankton and microphytobenthos biomasses and fluxes

These results are presented in Charpy-Roubaud (1988), Charpy-Roubaud *et al.* (1988), Le Borgne *et al.* (1989) and Blanchot *et al.* (1989). They are summarized in Table 3.

Results of the 5 experiments for determining the C/chl · a ratio appear in Table 4. This ratio ranged from 34 to 73 with an average of 50.

Table 4. Determination of the phytoplanktonic C/chl · a ratio in the lagoon of Tikehau. chl · a_{t0} = concentration (mg m^{-3}) at zero time; chl · a_{te} = concentration at $t0 + \delta t$ time; $\delta C/\delta t$ = carbon assimilation rate (mg C m^{-3} h^{-1})

Discussion

Planktonic trophic web

50% of the POC were in particles <5 μm.

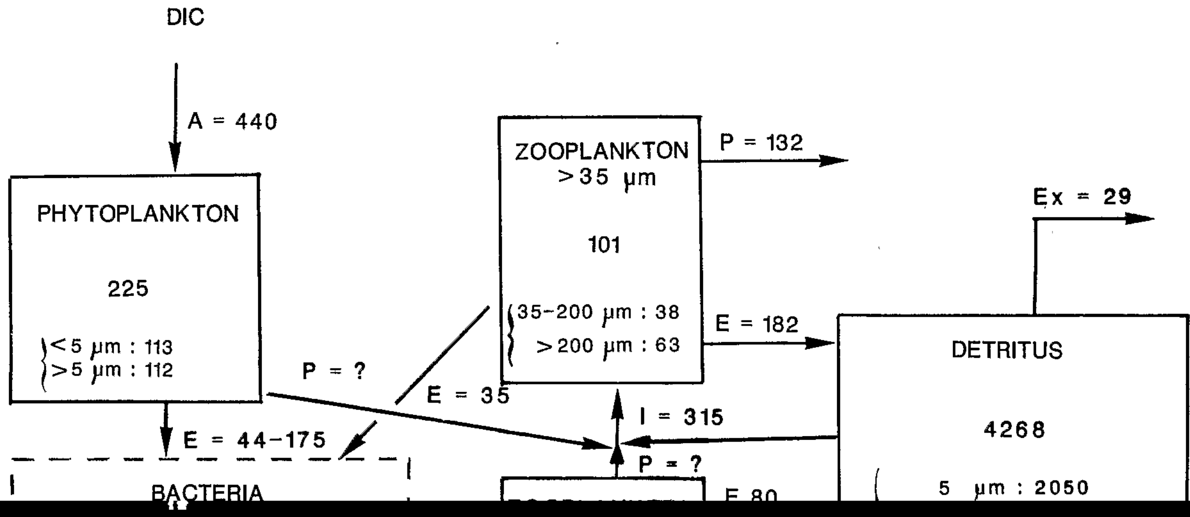
The detritus pool <35 μm can be estimated by the difference: POC – liv $C_{(<35\ \mu m)}$ = 192 – (0.11 × 250) = 164 mg C m^{-3}. Such a large proportion of detritic carbon in the POM is generally observed in tropical coastal waters: Gerber & Marshall (1982) found 77 to 84% of detritic carbon in the Enewetok lagoon, and Winn & Karl (1984) found 70 to 90% in the waters close to Hawaii.

We did not measure directly the biomass of with: *liv* $C_{(<5\,\mu m)}$ = percentage of $ATP_{(<5\,\mu m)} \times$ ATP $\times$ 250

phy $C_{(<5\,\mu m)}$ = percentage of $chl \cdot a_{(<5\,\mu m)} \times$ chl.a $\times$ (C/chl $\cdot\, a$ ratio).

The average value C/chl $\cdot\, a$ = 50 (from Table 4) lies within the range reported by Takahashi *et al.* (1985) for picoplankton and is very close to the ratio of 46 found by Laws *et al.* (1987) for oligo-

higher than the phytoplankton C in the Tikehau lagoon. Dominance of bacterial biomass was also observed in the oligotrophic waters of the Sargasso Sea by Fuhrman *et al.* (1989); the interpretation of these authors was that bacteria consume significant amounts of carbon probably released from phytoplankton directly or via herbivores. In Tikehau, the excretion rate of dissolved


DIC
A = 440
PHYTOPLANKTON
225
<5 µm : 113
>5 µm : 112
ZOOPLANKTON
>35 µm
101
35-200 µm : 38
>200 µm : 63
P = 132
Ex = 29
E = 182
DETRITUS
4268
5 µm : 2050
P = ?
E = 35
I = 315
E = 44-175
P = ?
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cant and the detritus pool originates from lagoonal primary productions.

The role of the phytoplankton: In spite of a low biomass (225 mg C m^{-2}), phytoplankton production is relatively high (440 mg C m^{-2} day^{-1}). The annual mean assimilation number calculated by Charpy-Roubaud *et al.* (1988) was 9.8 mg C mg^{-1} chl · *a* h^{-1}. This value is high but commonly observed in tropical coastal waters. Indeed, Takahashi & Bienfang (1983) gave an assimilation number of 8.09 mg C mg^{-1} chl · *a* h^{-1} for the picoplankton of the coastal Hawaiian waters; however, this value remains lower than the maximum potential production per chl · *a* observed by Legendre *et al.* (1988) in waters close to Moorea Island (French Polynesia): 5 to 25 mg C mg^{-1} chl · *a* h^{-1}.

The role of the zooplankton: The mesoplankton (200–2000 μm), microzooplankton (35–200 μm) and nanozooplankton (5–35 μm) biomasses are not very different: 63, 38 and 46 mg C m^{-2}. They represent in total 26% of the heterotrophs. In April 1986, Le Borgne *et al.* (1989) calculated the assimilation efficiency for mixed copepods ($D = 0.9$) and the net growth efficiency of carbon ($K_2 = 0.21 - 0.46$). The gross growth efficiency (K_1) is equal to the product of the assimilation efficiency, D, by the net growth efficiency, K_2 (Le Borgne, 1978). The high values of K_1 (19%–41%) could explain the rapid zooplankton turnover (one day). Zooplankton (35–2000 μm) ingestion is in the same order as the phytoplankton production and probably regulates its biomass. The zooplankton production (> 35 μm): 132 mg C m^{-2} day^{-1} represents the net pelagic production of the lagoon, available for the fish.

The role of the microphytobenthos: Microphyte biomass was higher in the benthos than in the plankton; however, production was lower in the benthos. Charpy-Roubaud *et al.* (1988) have demonstrated that phytobenthos production decreased with depth, while phytoplankton production increased (integrated production), but the sum remained constant. Phytobenthic production appears to be lower than the detritus sedimentation which probably makes a major contribution to the benthic food web. The biomass of the animals living in the sediments is not known, but they probably ingest the phytobenthic production plus a large part of the organic carbon sedimentation. Indeed, the organic C content of the interstitial waters of the sediments in Tikehau is very low 0.5 mg C g^{-1} of dry sediment (Sarazin *et al.*, 1988).

Conclusions

The detritus < 35 μm represent the most important particulate organic carbon pool in the lagoon. They originate from lagoonal primary production, and their sedimentation onto the bottom exceeds benthic primary production. Planktonic bacteria biomass is in the same order as the microphytobenthos, and is equal to twice the phytoplanktonic biomass. We interpret pelagic bacteria dominance by a 'microbial loop', returning energy released as DOM by phytoplankton and zooplankton, but also energy released as mucus from lagoonal coral communities.

Direct measurements of bacterial biomass, bacterial and nanozooplankton productions and nanoplankton and phytoplankton excretions could complete this carbon cycle.

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