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Plankton biomass and production in an open atoll lagoon: Uvea, New Caledonia

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Abstract

Uvea lagoon is an atoll-type one with a discontinuous belt of small islets on its western part and the main island to the east. Its depth increases steadily from east to west. A 2 week cruise in September 1992 aimed to study the ways in which these morphological features influence the functioning of the lagoon pelagic ecosystem. Hydrological parameters present a fair homogeneity, both horizontally and vertically over the whole lagoon, which is due to an efficient mixing and important exchanges with the oligotrophic open ocean. Lack of significant nutrient concentrations (NO_3, NO_2, NH_4, PO_4, SiO_3) in the water mass is in agreement with low planktonic biomasses: Chlorophyll *a* (Chl *a*) concentration is 0.233 mg m^{-3}, and ash-free dry weight is 5.25 and 7.55 mg m^{-3} for [35–200 μm] and [200–2000 μm] size fractions respectively. These biomass levels are more than twice the concentration of the surrounding open ocean. Total Chl *a* is dominated by the >1 μm size-fraction, thus contrasting with the dominance of small cells (<1 μm) in the open ocean. Phytoplankton prevails in the [35–200 μm] size-class, indicating the occurrence of microphytobenthos brought by mixing of the water column. The [200–2000 μm] fraction is made up primarily of copepods (61% of the dry weight), appendicularians and radiolarians. Planktonic predators, such as chaetognaths are almost absent. Three different methods dealing with carbon production, i.e., ^{14}C fixation, in-bottle O_2 production, and natural O_2 variations, lead to a coherent estimate of pelagic primary production: 27.5 mg C m^{-3} d^{-1}. Half of this production is achieved by <1 μm cells. Zooplankton production, which was assessed by the C/N/P ratios method, is equal to 10.4 mg C m^{-3} d^{-1} and its P:B ratio is 114%. On the whole, Uvea lagoon appears to be oligotrophic compared with other ones, because it is wide-open. © 1997 Elsevier Science B.V.

Keywords: Atoll; Phytoplankton; Zooplankton; Biomass; Production rate

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1. Introduction

Located in the northwest of the Loyalty archipelago (New Caledonia Exclusive Economic Zone), Uvea is the largest (839 km^2) atoll-like island in a radius of more than 2000 km. This characteristic led the Centre ORSTOM of Noumea to make a preliminary study on its lagoonal aquatic living resources. In order to gain understanding of the ichthyofauna distribution and to assess its potential production, an original field study, focused on hydrology and plankton, was performed during the PLOUVEAL cruise in September 1992.

Uvea lagoon is encircled by a crown of islands. It can be divided in two parts (Fig. 1). The eastern part is shallow and protected from the prevailing southeasterly winds by the main island. The western part is deeper and wide open towards the deep ocean. The bottom is mainly composed of limestone slabs covered with a thin layer of sand (Chevillon et al., 1992). All these features are likely to influence exchange with the open ocean and interactions with the benthic community. To take these influences into account, the sampling strategy was based on a network of lagoonal stations at various depths, complemented by sampling in the surrounding open ocean.

This paper presents a detailed account of the hydrology and plankton abundances. The main qualitative and quantitative characteristics of the plankton biomass and of its horizontal and vertical distributions in Uvea lagoon are also analyzed. Such a description, considering in particular, the size structure, taxonomic composition and chemical constituents, allows us to define the functioning scheme of the pelagic ecosystem and its degree of stability. Based on such observations, we give a tentative estimation of the ichthyofauna potential production. Since the conclusions presented here apply to a 2 week cruise only, we discuss the possibility to extrapolate from them for a longer period.

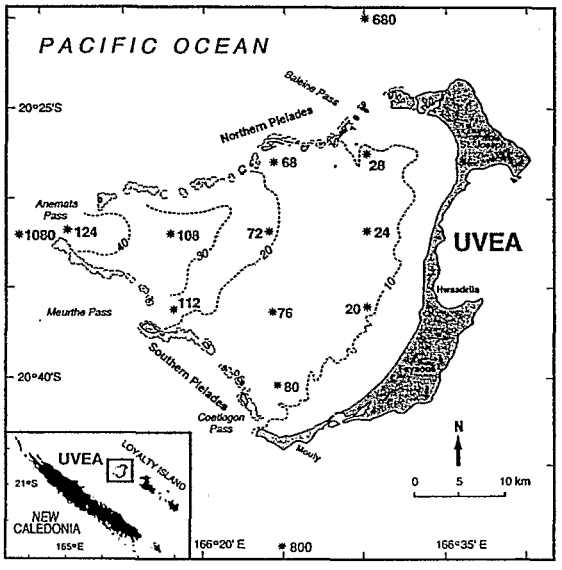

Fig. 1. Location of sampling stations and bathymetry in the lagoon of Uvea (Loyalty archipelago, New Caledonia EEZ).

2. Materials and methods

The PLOUVEAL cruise was undertaken in Uvea lagoon from September 4 to 17, 1992 onboard research vessel 'Alis'. The lagoon can be divided into three bathymetric regions: 0–10 m (25% of lagoon area), 10–20 m (49%), and >20 m (26%). Ten stations, located in the two latter sectors (Fig. 1), were successively sampled four times per day, in order to take diel variations into account. The following stations were sampled sequentially: 112, 124, 20, 108, 72, 68, 24, 80, and 76. It may be noticed that the tide effect was negligible since the tidal amplitude in the region is small, maximum between low and high tides being equal to 1.1 m in September. For each site of the lagoon, CTD casts were made every morning with a SeaBird SEA CAT SBE-19-01 probe. Discrete water samples were collected at 5–10 m depth intervals three times per day (5:00, 14:00, 18:00) with 5 l Niskin bottles, and once per day (9:00) with a 60 l bottle. Lagoon observations were compared with data of three reference stations, located in the surrounding open ocean at 15:00. Additionally, 11 samples were also taken from the first 20 cm above the bottom, with a 5 l bottle closed manually by a diver. The bottom samples were taken near the Baleine pass, north of the lagoon, on various biotopes (sand, caves, pinnacles, beachrock).

Photosynthetically available radiation (PAR) profiles were obtained at noon, using two Li-Cor quantameters. The overall daily radiative energy was integrated with a third quantameter.

Dissolved oxygen was measured with a YSI 50B probe, calibrated every evening with the Winkler method using a Metrohm titroprocessor 686. Nutrients (NO_3, NO_2, NH_4, PO_4, SiO_3) were analysed immediately at sea with a Technicon autoanalyzer II, following the methods described by Strickland and Parsons (1972) and, for NH_4, by Slawyk and Mc Isaac (1972). For NO_3 concentrations <1.5 μM and NO_2, the high sensitivity (H.S.) method of Oudot and Montel (1988) was used. The lower limits of detection of the different analyses are: 0.01 μM for NO_3 and NO_2 (H.S method), 0.03 μM for PO_4, 0.05 μM for NH_4 and 0.1 μM for SiO_3. Total dissolved nitrogen (N_{total}) and phosphorus (P_{total}) were measured after UV mineralization (2.5 h), using the Armstrong and Tibbitts (1968) method.

Seston C, N, P elemental composition and mass were measured on 1030 ml sea-water samples, sieved through 35 μm nylon silk, and filtered on precombusted Whatman GF/F (400°C, 12 h). Phosphorus was analysed on board, according to the sodium persulfate method of Menzel and Corwin (1965). Carbon and nitrogen samples were processed at Centre ORSTOM de Noumea after deep-freezing preservation, with a Perkin-Elmer 2400 CHN analyser at 1100°C. Percentage contribution of organics to total carbon was determined on seston filters, after exposure to HCl vapours during 12 h.

Chlorophyll *a* (Chl *a*) and pheopigment (Pheo) measurements were made by fluorometry on samples filtered through GF/F filters, after extraction in 95% methanol (Le Bouteiller et al., 1992). Analyses were performed on unfractionated or fractionated samples obtained after pre-filtration on 0.8, 1, 3, 5, 8, and 10 μm porosity Nuclepore filters. %Pheo refers to the Pheo/(Pheo + Chl *a*) ratio.

Phytoplankton cell counts were made at five stations (28, 68, 76, 108 and 124) on Irgalan black Nuclepore filters (0.2 μm) by epifluorescence microscopy as described by Blanchot et al. (1989).

Primary production was measured in situ for 11 h (sunrise to sunset) or for 3 h (around noon), on 300 ml flasks attached to a moored line. Three different methods were used in parallel: ^{14}C uptake, chlorophyll increase, and oxygen production. (1) The ^{14}C fixation samples were incubated after adding 148 kBq ^{14}C-bicarbonate. An initial sample was inoculated with ^{14}C and filtered immediately to determine adsorption. At the end of incubations, samples were filtered onto GF/F, rinsed with filtered sea water and kept in a deep-freezer before counting with a Packard Tri-Carb 300 C scintillation counter. Some flasks were incubated in the dark: their ^{14}C uptake represents less than 5% of the light fixation. ^{14}C uptake coefficient of variation was 2.4–8.6% ($n = 9$). Production was measured on total and size-fractionated samples. (2) Chlorophyll production was taken as the difference between morning and evening concentrations in light bottles, no significant change being observed in the dark samples during the incubation. (3) Net oxygen production values refer to the observed oxygen increase during the incubation period in light bottles, and gross production, to the difference between the light and dark values at the end of the experiments.

Zooplankton was sampled three times per day (7:00, 14:00, and 20:00) on vertical hauls from the bottom to the surface with triple 200 μm WP-2 (UNESCO, 1968) and 35 μm nets (Blanchot et al., 1989). Filtered volume was given by TSK flow-meters. All zooplankton samples were sieved through 2 mm or 200 μm metal grids from one or three nets of the WP-2 or 35μm, to generate 200–2000 μm and 35–200 μm size fractions. Biomass samples were collected on preweighed silks, rinsed with 100 ml freshwater, dried at 60°C for 24 h, and deep-frozen until weighing (±0.1 mg) to obtain the dry weight (DW). Ash-free dry weight (AFDW), a proxy of organic matter, was subsequently obtained after a 1.5 h combustion at 550°C.

Zooplankton C, N, P composition was measured on one of the three nets. The whole catch was diluted as follows: plankton was ground in a Potter mill, diluted in distilled water and two subsamples were poured into 100 μl aluminium boats, processed like dry weight samples and analysed according to the methods described above for seston.

Mesozooplankton (> 200 μm) originating from one of the three nets, was counted on the whole sample preserved in 10% formaldehyde, except for the copepods which were diluted according to Frontier (1972). Although preservation affects dry weight values, the diminution may be considered as similar for major taxa after a minimum of six months in formaldehyde. Contributions of the taxa are, therefore, equal to those of fresh samples (Le Borgne and Roger, 1983). Major taxa were sorted and weighed with a Perkin-Elmer electrobalance. Copepods determination was performed on 10 samples in order to identify the dominant species. Microzooplankton (35–200 μm) was diluted and a volume of 2 ml was counted with an inverted microscope.

Zooplankton respiration and excretion (NH_4, PO_4, N_{total}, P_{total}) data were obtained according to the procedure described by Le Borgne et al. (1989). Incubations were performed in situ during ~10 h, in 1 l flasks filled with filtered water, inoculated with unsorted living zooplankton. Metabolic rates refer to 24 h and to 1 mg of zooplankton dry weight. Zooplankton production was calculated from excretion (T) using the net growth efficiency (K_2), as follows:

$$P = TK_2(1 - K_2)^{-1} \quad (1)$$

$K_{2,N}$ and $K_{2,P}$, for nitrogen and phosphorus, respectively, were calculated by the C/N/P ratios method (Le Borgne, 1978), which is based on the typical differences in C/N/P ratios of zooplankton constituents, its metabolic losses, and its prey:

$$K_{2,P} = (a_1 - a_2)\,(a_3 - a_2)^{-1} \tag{2}$$

$$K_{2,N} = K_{2,P}\,a_3\,(a_1)^{-1} \tag{3}$$

with: a_1 = particulate (<35 μm) N/P ratio; a_2: zooplankton N/P excretion ratio; a_3 :zooplankton N/P constitution ratio.Ingestion (I) is inferred from P and T using the assimilation efficiency (D):

$$I = (P + T)D^{-1} \tag{4}$$

3. Results

This paper only presents the general results of the study. Readers can obtain the complete information from the data report (Le Borgne et al., 1993).

3.1. Hydrology

The mean temperature in the lagoon in September is 23.5°C, slightly lower than in the mixed layer of the open ocean (23.4–24.1°C, Table 1). The salinity is, on average, the same inside, and outside, the lagoon (35.56 psu). Salinity spatial distribution is marked by a very low variability: thus, salinity on the eastern side, near the main island, is only slightly higher (35.60–35.66 psu) because evaporation effect is more effective in shallow waters. Temperature and salinity do not display any vertical gradient from surface to bottom, except at the westernmost stations (Fig. 2) where low temperature and

Table 1
Mean values and standard deviation (S.D.) of temperature (°C), salinity (psu), oxygen (ml l^{-1}) and nutrients (μM) in Uvea lagoon and in the surrounding open ocean. n = number of samples

Parameter	Lagoon						Open ocean		
	Bottom			Water column			0–40 m		
	Mean	S.D.	(n)	Mean	S.D.	(n)	Mean	S.D.	(n)
Temperature				23.50	0.23	(217)	23.63	0.19	(18)
Salinity				35.56	0.05	(217)	35.55	0.01	(18)
NO_3	0.236	0.094	(9)	0.016	0.015	(126)	0.003	0.002	(11)
NO_2	0.026	0.006	(9)	0.003	0.003	(120)	0.002	0.001	(11)
NH4	0.14	0.01	(9)	0.04	0.06	(126)	0.07	0.08	(11)
PO4	0.07	0.01	(9)	0.05	0.03	(126)	0.05	0.01	(11)
SiO_3	0.43	0.06	(9)	0.57	0.19	(33)	0.72	0.10	(11)
Oxygen				4.922	0.130	(70)			

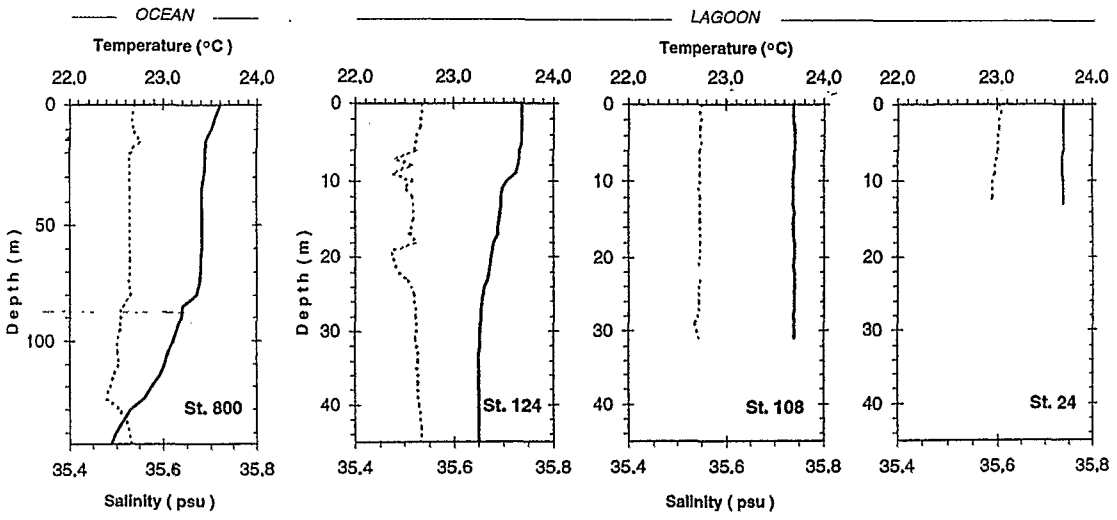

Fig. 2. Vertical profiles of temperature (solid line) and salinity (dotted line), in and outside the lagoon. Illustrated stations are representative of the lagoon (Staation 24, 108, 124) and the surrounding open ocean (Station 800).

salinity variations are probably linked to tidal currents. Such homogeneity in vertical profiles is the consequence of efficient mixing during the cruise.

The water column nutrient concentrations in the lagoon listed in Table 2 are very low (often close to the detection limits), and similar to the concentrations in the upper layer of the open ocean (Table 1), which are typically nutrient-depleted down to the bottom of the mixed layer (~80 m). Geographical and vertical nutrient distributions are relatively homogeneous and concentrations display no variations between morning and evening casts. Interestingly, bottom samples, collected by diving, present higher concentrations, except for silicate (Table 1).

Concentrations of dissolved oxygen range from 4.171 to 5.078 ml l^{-1} (Table 3), and display no particular distribution pattern. Systematic diel variations are observed at all depths (except at St. 68), with a 0.3–8% increase between 5:00 and 18:00 due to photosynthetic activity.

3.2. Seston biomass and phytoplankton production

3.2.1. Pigment concentrations, size distribution, and cell counts

Mean Chl *a* concentration in the lagoon is 0.233 mg m^{-3} (mean of 39 profiles obtained at 10 stations, S.D.=0.076), which is twice as much as in the mixed layer of the surrounding open ocean (Chl a=0.100 mg m^{-3}). Chl *a* concentration increases slightly from the surface to the bottom (Fig. 3) at the deep stations (>20 m). A significant inverse correlation ($r=-0.91$, $n=5$) is observed between Chl *a* concentrations in the 0–10 m upper layer and bathymetry (Fig. 6). Whereas the 0–10 m Chl *a* content is greater at the shallow stations, it is comparable to the oceanic surface values at the deep stations of the western part of the lagoon. In contrast, water column integrated Chl *a* content is positively correlated with depth (Fig. 6).

The size distribution of Chl *a* indicates that the >1 μm fraction predominates in the

Table 2
Nutrients and particulate carbon, nitrogen and phosphorus: mean values from morning, noon and evening casts

Depth (m)	NO_2 (μM)	NO_3 (μM)	PO_4 (μM)	NH_4 (μM)	SiO_3 (μM)	Particulate C (μM)	Particulate N (μM)	Particulate P (μM)
Station 20								
0	0.003	0.014	0.05	0.10	0.35	10.05	0.99	0.058
5	0.002	0.016	0.03	0.05	0.42	8.27	0.94	0.055
10	0.004	0.022	0.03	0.00	0.39	8.56	1.14	0.049
Station 24								
0	0.002	0.004	0.016	0.13	0.59			0.063
5	0.002	0.002	0.017	0.02	0.69	9.04	0.94	0.061
10	0.002	0.002	0.015	0,00	0.60	8.39	0.93	0.063
Station 28								
0	0.008	0.008	0.02	0.02	0.51			0.060
5	0.005	0.011	0.01	0.01	0.45			0.058
10	0.006	0.008	0.01	0.00	0.28	6.31	0.69	0.056
Station 80								
0	0.006	0.052	0.042	0.02				0.028
5	0.006	0.052	0.042	0.12		5.19	0.47	0.031
10	0.006	0.052	0.040	0.01		4.95	0.57	0.032
14						4.69	0.48	0.026
Station 68								
0	0.001	0.011	0.02	0.01	0.59			
5	0.001	0.014	0.03	0.02	0.87	4.67	0.53	0.044
10	0.005	0.028	0.03	0.02	0.78	5.14	0.54	0.041
15	0.009	0.025	0.03	0.00	0.81	6.08	0.63	0.047
Station: 72								
0	0.002	0.001	0.05	0.00	0.57	5.57	0.60	0.049
5	0.002	0.006	0.07	0.01	0.56	4.08	0.56	0.037
10	0.002	0.001	0.04	0.01	0.52	4.60	0.53	0.043
15	0.003	0.005	0.03	0.02	0.35	5.62	0.67	0.041
Station 76								
0	0.003	0.004	0.038	0.02	0.34			0.059
5	0.002	0.002	0.032	0.01	0.50	10.34	1.12	0.054
10	0.002	0.003	0.032	0.05	0.53	7.80	0.97	0.045
15	0.002	0.004	0.032	0.01	0.44	10.59	1.53	0.054
Station 108								
5	0.006	0.022	0.05	0.05	0.76	4.16	0.46	0.032
10	0.004	0.024	0.06	0.02	0.88	3.20	0.35	0.038
15	0.002	0.033	0.08	0.01	0.80	3.58	0.67	0.003
20	0.003	0.032	0.07	0.05	0.84	4.37	0.51	0.037
25	0.004	0.029	0.06	0.02	0.52	5.08	0.43	0.003
30	0.005	0.040	0.07	0.03	0.84	4.20	0.45	0.032
Station: 112								
0	0.001	0.005	0.08	0.16	0.52			
5	0.001	0.006	0.07	0.07	0.92	4.26	0.40	
10	0.003	0.019	0.07	0.00	0.44	5.35	0.50	0.025
15	0.001	0.011	0.06	0.04	0.24			
20	0.001	0.010	0.06	0.07	0.36	6.20	0.64	0.021
25	0.002	0.021	0.06	0.14	0.24	6.09	1.08	0.022

Table 2. Continued

Depth (m)	NO_2 (μM)	NO_3 (μM)	PO_4 (μM)	NH_4 (μM)	SiO_3 (μM)	Particulate C (μM)	Particulate N (μM)	Particulate P (μM)
Station: 124								
5	0.001	0.016	0.07	0.01		6.23	0.63	0.019
10	0.001	0.020	0.07	0.00				0.003
20	0.001	0.015	0.06	0.00		8.85	1.19	0.029
30	0.003	0.032	0.07	0.04		5.25	0.595	0.027
35	0.005	0.028	0.06	0.04		6.62	0.69	
40	0.005	0.028	0.09	0.13		3.40	0.33	0.025

Table 3
Oxygen concentrations (ml/l^{-1}) at dawn (5:00) and dusk (18:00) in Uvea lagoon

Depth	Station 20		Station 24		Station 28		Station 80	
	05:00	18:00	05:00	18:00	05:00	18:00	05:00	18:00
0	4.946	5.013	4.936	5.015	4.931	4.948	4.921	4.958
5	4.965	5.024	4.907	5.018	4.895	4.934	4.912	4.975
10	4.965	5.008	4.891		4.878		4.655	
Depth	Station 72		Station 68		Station 76		Station 108	
	05:00	18:00	05:00	18:00	05:00	18:00	05:00	18:00
0	4.856	4.918			4.976	5.034		
5	4.529	4.904	4.884	4.859	4.891	5.062	4.878	
10	4.171		4.832	4.825	5.002	5.069		
15			4.850		4.960	5.078	4.859	4.885
25							4.842	4.846
30							4.798	

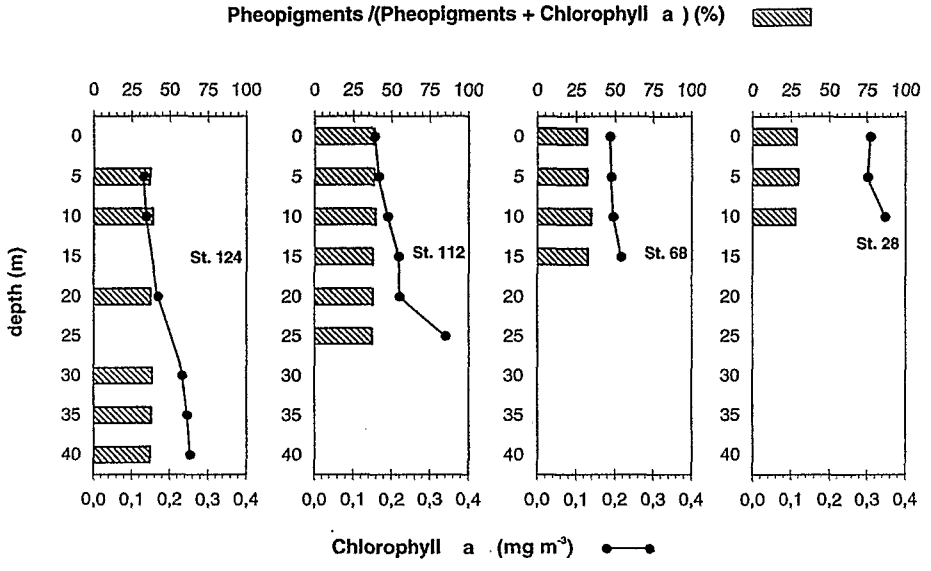

Fig. 3. Vertical profiles of phytoplankton characteristics at five representative stations: (a) Chl *a* concentration and percent contribution of pheopigments to total pigments.

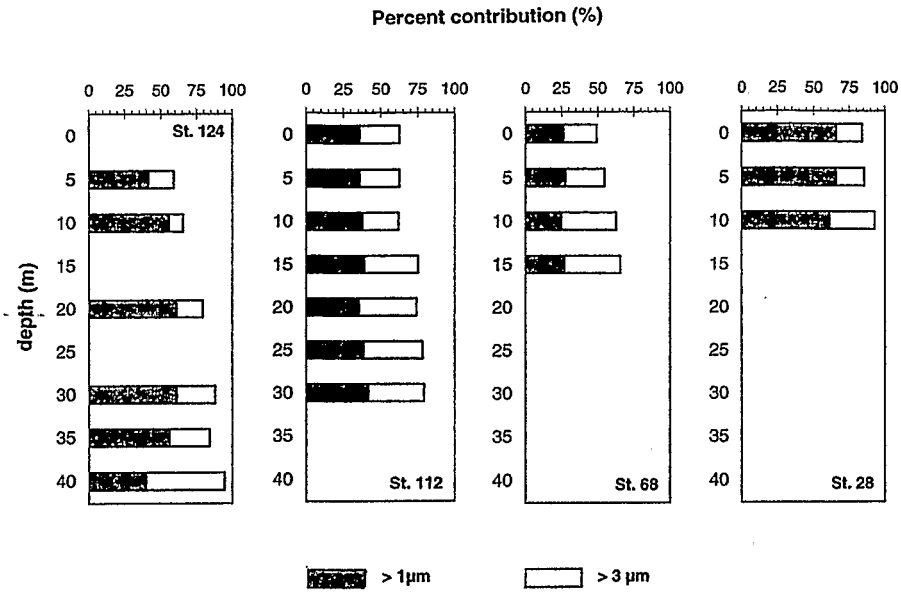

Fig. 4. Vertical profiles of phytoplankton characteristics at five representative stations: Chl *a* size-structure.

lagoon and accounts for 50–80% of the total Chl *a* (26–65% in the >3 µm fraction, Fig. 4). Such a pattern contrasts with that observed in the tropical open ocean, characterized by the dominance of the <1µm fraction in the nutrient depleted layer (Le Bouteiller et al., 1992). Size distribution is highly variable from one sample to another, and no general pattern can be found, except at the deep stations (112 and 124) where the >1 µm size increases from the surface to the bottom. Part of this variability is probably due to temporary occurrences of significant amounts of *Trichodesmium* and large microphytobenthos cells, which are also sampled by 35 µm plankton nets. According to the cell counts (Fig. 5), cyanobacteria predominate at all stations, particularly at station

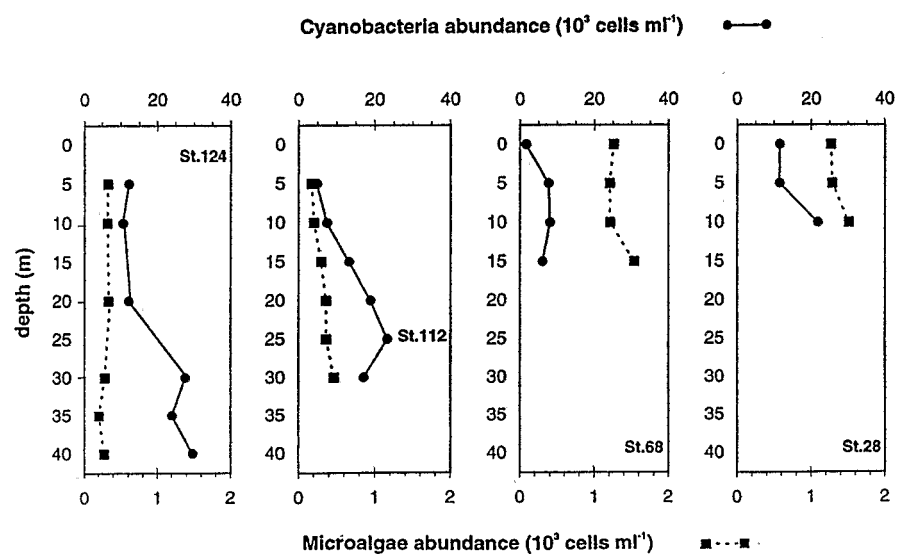

Fig. 5. Vertical profiles of phytoplankton characteristics at five representative stations: cyanobacteria and microalgae cell abundances (by courtesy of J. Blanchot).

76 where counts were made impossible due to the presence of many cyanobacteria aggregates. Their numerical abundance is larger at the shallow stations (up to 25 000 cells ml^{-1}) than at the deeper ones (4000–7000 cells ml^{-1}). Microalgae are much less abundant (200–1400 cell ml^{-1}). Their highest concentrations are found below 20 m, in agreement with the increasing importance of Chl $a>1$ μm with depth, mentioned before.

There are two main trends in the pheopigment data. Firstly, the %Pheo is minimum (31%) on shallow depths and maximum (38%) at the deep stations (Fig. 3). Secondly, this %Pheo is lower in the >1 μm size fraction. These results confirm the predominance of large cells at the shallow stations, which probably originate from the bottom.

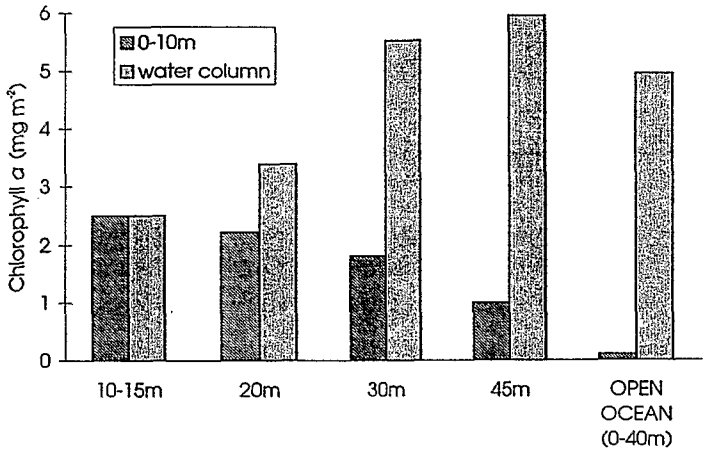

Fig. 6. Integrated Chl *a* concentrations (mg m^{-2}) in the lagoon as a function of bathymetry, and comparison with the surrounding open ocean. Chl *a* values are integrated over 0–10 m and over the whole water column.

3.2.2. Particulate matter

No general distribution scheme can be defined for particulate carbon, nitrogen and phosphorus concentrations (Table 2). The range for carbon is 3.2–10.6 μM C m^{-3}, with highest values (>8 μM C l^{-1}) observed generally at the shallow stations, due to the mixing of bottom particles. Carbonate percentage averages 10.2% of total carbon, with a high variability (sd=25.3%). Mean mass C/N and N/P ratios are 7.2 and 15.1, respectively.

3.2.3. Primary production

Average hourly primary production (^{14}C fixation), computed from in situ 11 h incubations, is 2.5 mg C m^{-3} h^{-1} (Table 4), corresponding to a daily production of 27.5 mg C m^{-3} d^{-1}. The mean ^{14}C uptake rate normalized to initial chlorophyll (i.e., productivity) is 10.7 g C/g Chl *a* h^{-1} with maxima observed at the two deepest stations (Stations 124 and 108). Shorter incubations over the 2–3 h interval between 10:00 and 13:00 gave significantly higher ^{14}C fixation rates and productivity: 3.2 mg C m^{-3} h^{-1} and 12.8 g C/g Chl *a* h^{-1}. This result can be easily explained because the rates measured during short incubations are closer to gross production than the 11 h incubation values, which are more representative of net production.

Table 4
Comparison of net and gross O_2 primary production with ^{14}C uptake (mg C m^{-2} h^{-1})

Station	Layer	Net O_2 production	Gross O_2 production	C^{14} production
20	0–10 m	22.50	30.63	38.77
24	0–10 m	30.48	36.08	21.28
28	0–10 m	11.48	32.40	26.33
80	0–10 m	26.60	37.98	23.80
72	0–15 m	22.35	39.15	23.40
68	0–15 m	34.90	52.35	33.38
76	0–15 m	30.00	56.48	32.78
112	0–25 m	44.25	83.25	61.60
108	0–30 m	26.35	37.45	91.17
124	0–40 m			98.10

In bottle O_2 productions are converted into carbon with PQ=1.25 (see Section 2).

No effect of light on carbon production could be detected. Despite the high irradiance values at 5 m (1.5–2.7 E m^{-2} h^{-1}), no near-surface photoinhibition was observed as it is commonly reported in the open ocean (Le Bouteiller and Herbland, 1984; Cullen et al., 1992). The absence of photoinhibition near the surface, however, has been reported in Tikehau atoll by Charpy-Roubaud and Charpy (1994). No light effect on deeper samples was noted, either, thus showing light was not limiting: at the deepest levels, a minimum of 0.5 E m^{-2} h^{-1} was measured by quantametry. It is important to notice that the upward light, i.e., the light reflected by the bottom, was not taken into account although it represents probably a great part of the energy received by the samples, particularly on the white sandy bottoms which cover more than half of the lagoon. The high values of ^{14}C fixation and productivity calculated from the 11 h incubation experiments, suggest that the phytoplankton energetic needs were satisfied under the good weather conditions which prevailed during our study (mean daily irradiance >30 E m^{-2} d^{-1}).

Half of the ^{14}C uptake is due to the <1 μm size fraction, although it represents only 20–50% of the total Chl *a*, indicating that productivity is higher for the small cells than

Table 5
Total and <1 μm chlorophyll *a* concentrations (mg m^{-2}) at the beginning (*to*) and the end (*tf*) of primary production incubations

Station	Layer	Chl *a* <1 μm		Total Chl *a*	
		to	*tf*	*to*	*tf*
20	0–10 m			2.54	4.00
24	0–10 m	0.87	1.22	2.40	2.89
28	0–10 m	0.68	0.62	2.46	3.02
80	0–10 m			2.64	3.28
72	0–15 m			2.49	3.06
68	0–15 m			3.25	3.31
76	0–15 m	1.83	2.31	4.42	5.05
112	0–25 m	1.62	1.47	5.66	6.76
108	0–30 m			5.39	7.81
124	0–40 m	1.25	2.26	5.95	7.99

Table 6
[200–2000 μm] size-class biomass, AFDW day/night ratio, elemental and taxonomic composition with respect to depth

Depth range (m)	10–15 m				20 m			30 m			45 m		
Station	20	24	28	80	68	72	76	108		112	124		
					11.5	13.9	7.9	21.8		7.3	3.4		
AFDW (mg m^{-3})	17.7	8.3	8.8	2.3	47.3	72.9	16.8	73.5		41.5	66.7		
Day/Night ratio (%)	15.2	19.7	98.0	41.2	30.1	31.4	25.8	33.3		30.5	32.4		
%AFDW	54.7	73.7	65.6	40.9	73.3	74.7	58.6	81.2		73.9	71.3		
%C	27.3	28.3	30.7	19.4	5.7	6.1	4.7	6.8		6.2	4.4		
%N	4.4	5.2	6.7	2.6	0.72	0.77	0.54	0.86		0.77	0.85		
%P	0.74	0.69	0.66	0.38									
	No./m^3	% of Total	DW (%)		No./m^3	% of Total	DW (%)	No./m^3	% of Total	DW (%)	No./m^3	% of Total	DW (%)
Number of samples	6	6	2		6	6	1	2	2	1	1	1	1
Trichodesmium	425.1 (374.9)	33.0	7.8		104.8 (40.6)	10.0	1.7	101.2 (117.0)	6.0	0.2	61.8	9.0	1.8
Other phytoplankton	25.9 (11.6)	2.0	0.4		28.0 (8.4)	2.7	0.8	60.4 (45.9)	3.6	0.8	45.9	6.7	1.3
Radiolaria-.Acantharia	83.2 (120.5)	6.5	3.1		261.2 (377.9)	25.0	0.4	32.8 (3.6)	2.0	0.7	50.0	7.3	2.9
Foraminifera	6.9 (5.6)	0.5	1.0		10.7 (4.4)	1.0	0.5	24.3 (27.2)	1.4	1.3	0.7	0.1	0.0
Total Protists	541.1 (489.5)	42.1	12.3		404.8 (406.2)	38.8	3.4	218.6	13.0	3.0	158.4	23.2	6.0

Copepoda	564.5 (824.5)	43.9	32.8	557.5 (222.8)	53.4	64.2	1296.2 (754.5)	77.1	64.5	397.7	58.1	59.2
Ostracoda	1.0 (2.4)	0.0	0.0	1.0 (1.6)	0.0	0.0	1.6 (1.3)	0.0	0.4	0.9	0.1	0.4
Larval Decapods	6.2 (4.9)	0.5	5.8	9.8 (6.8)	0.9	1.1	16.4 (3.0)	1.0	5.8	2.9	0.4	2.9
Larval/adults Euphausiids	0.1 (0.2)	0.0	0.0	0.1 (0.1)	0.0	0.0	4.0 (4.1)	0.2	3.0	0.9	0.1	0.6
Larval Molluscs	4.2 (4.6)	0.3	0.4	0.5 (0.5)	0.0	0.0	2.4 (2.0)	0.1	0.1	2.1	0.3	0.2
Pteropoda	61.0 (0.0)	3.6	3.1	7.9 (0.0)	1.9	1.9	2.1 (0.0)	1.4	1.6	13.7	2.1	2.5
Appendicularia	102.2 (80.9)	7.9	9.3	43.7 (22.5)	4.2	6.2	110.3 (47.7)	6.6	10.7	94.8	13.9	15.8
Miscellaneous	4.7 (5.6)	0.4	0.6	1.2 (1.8)	0.1	0.0	0.8 (0.9)	0.0	0.0	0.9	0.1	0.2
Total particle-feeders	728.6 (907.4)	56.6	52.0	621.7 (231.8)	59.5	73.4	1452.7	86.4	86.1	513.9	75.1	81.8
Hydromed.- Syphonoph.	2.3 (3.4)	0.2	0.7	5.5 (6.6)	0.5	0.4	5.6 (8.0)	0.3	0.9	5.0	0.7	1.2
Chaetognatha	0.8 (1.1)	0.0	0.3	1.0 (1.2)	0.0	0.7	4.2 (6.0)	0.3	4.0	2.2	0.3	2.0
Larval Brachyura	3.2 (3.5)	0.3	1.3	2.0 (1.5)	0.2	0.1	3.8 (5.4)	0.2	1.4	0.4	0.0	0.1
Amphipoda	3.3 (0.4)	0.3	0.0	3.1 (6.1)	0.3	0.0	0.2 (0.3)	0.0	0.2	0.3	0.0	0.3
Miscellaneous	5.8 (0.2)	0.5	1.1	1.1 (1.0)	0.1	0.2	3.3 (4.7)	0.2	1.5	2.1	0.3	0.6
Total predators	14.2 (0.13)	1.1	3.3	12.6 (11.1)	1.2	1.5	17.18	1.0	8.0	10.1	1.5	4.2
Fish eggs	2.6 (0.14)	0.2	2.0	0.7 (0.4)	0.0	0.2	1.3 (1.9)	0.0	0.3	1.8	0.3	0.4
Detritus			32.4			21.6			2.9			7.9

%AFDW, %C, %N, %P refer to DW. No./m^3 is the average density of any taxa with standard deviation in brackets, % of total, its numerical contribution, and DW(%), its weight contribution in the whole sample.

for the larger ones. A significant increase of Chl *a* is observed in experimental light flasks during the 11 h incubations. This increase is on average 20–25% for total Chl *a* and 50% for the Chl *a*<1 μm (Table 5). We, therefore, conclude that the smallest size fraction is more efficient than the larger one, both in terms of C and Chl *a* production.

^{14}C fixation and oxygen production (in-bottle and natural oxygen variations) values lead to coherent carbon production estimations for Uvea lagoon (Table 4). For the upper 0–10 m, which is common to all stations, in-bottle O_2 variations allow us to estimate mean net and gross carbon productions of 1.9 and 3.1 mg C m^{-3} h^{-1}, respectively, using the photosynthetic quotient (1.25) of Williams et al. (1983). The ^{14}C fixation values for the 0–10 m layer (2.3 mg C m^{-3} h^{-1}) fall between net and gross production obtained with oxygen data. From the natural oxygen diurnal variations (see above), it is possible to calculate a mean in situ net production between 5:00 and 18:00 for the first 0–10 m which is equal to 0.63 l O_2 m^{-2} for daytime, i.e., 2.3 mg C m^{-3} h^{-1} (Table 4). This value is identical to the measured ^{14}C-fixation rate, and slightly higher than the net production obtained in the experimental flasks (1.9 mg C m^{-3} h^{-1}).

3.3. Zooplankton biomass and production

3.3.1. Biomass and composition (taxonomy and chemistry)

The biomass data on Tables 6 and 7, are presented as ash-free dry weights (AFDW) and are averaged on day and night hauls in order to take diel variations into account. Thus, for the vertical WP-2 net (i.e., >200 μm), daytime values are equal to 49% of nighttime ones, on average (Table 6). No significant difference, however, is observed for the smaller size-class (35–200 μm, Table 7).

Weighed mean biomass (i.e., taking the bathymetry into account) for the whole lagoon is 7.55 mg AFDW m^{-3} for the [200–2000 μm] size-class and 5.25 mg AFDW m^{-3} for the [35–200 μm]. The biomass distribution mirrors the bathymetry (Fig. 7), leading to a negative E–W gradient. Note that such an E–W gradient would be less obvious in terms of integrated biomass (per m^2), particularly for the smaller size-fraction. This ratio is comparable to the one observed for phytoplankton biomass (Fig. 6), but it can be considered as small compared to other studies. As shown in Fig. 7, the mean biomass value in the lagoon is higher than in the upper 0–40 m oceanic layer (lagoon/ocean ratio=2.4).

The taxonomic data for the >200 μm fraction at the lagoonal stations are summarized on Table 6. They reveal a high variability in the percentage contribution of each taxon and the unusual quasi-absence of Chaetognaths. Copepods are numerically dominant, especially at the deep stations (>20 m). The other important particle-feeders are: appendicularians (7% of total numbers) and radiolarians (11% of counts). In terms of DW, copepods represent more than half (61%) of the [200–2000 μm] fraction with five dominant species (D. Binet, pers. com.): *Centropages orsinii, Acartia australis, Oithona plumifera, O. nana, O. attenuata*. Except for *Candacia* sp. and *Onychocorycaeus* sp., all copepod species found in the open ocean are present in the lagoon. Table 6 shows also high concentrations of *Trichodesmium*. The highest abundances (up to 33.0% of counts,

Table 7
[35–200 μm] size-class biomass, AFDW day/night ratio, elemental and taxonomic composition with respect to depth

Depth range	10–15 m				20 m			30 m		45 m	
Station number	20	24	28	80	68	72	76	108	112	124	
AFDW (mg m^{-3})	2.9	7.2	8.6	6.3	7.8	13.2	6.8	4.2	2.9	2.1	
Day/Night (%)	42.3	80.2	84.4	93.1	131.7	124.1	50	112.6	116.2	102.9	
%AFDW	21.5	24.3	26.1	17.9	27.0	28.8	26.8	37.9	21.5	31.1	
%C			17.8	18.5	19.2	19.3	27.7	21.1	19.8	23.0	
%N			2.3	1.8	2.2	2.5	4.7	3.1	2.7	6.5	
%P			0.247	0.205	0.219	0.283	0.548	0.394	0.251	0.457	
Number of samples		2				1		1		1	
	No./m^3	S.D.	% of Total		No./m^3	% of Total		No./m^3	% of Total	No./m^3	% of Total
Diatoms	91.31	66.91	46.3		119.0416	71.8		4.15	21.6	8.51	30.4
Trichodesmium	4.83	4.70	2.4		6.17	3.7		0.30	1.5	3.16	11.3
Ceratium sp.	0.00	0.00	0.0		0.00	0.0		0.00	0.0	1.66	6.0
Noctiluca sp.	48.75	68.94	24.7		175.00	1.8		220.00	8.5	0.00	0.0
Other Dinoflagellates	8.78	3.30	4.5		13.17	7.9		1.94	10.1	1.87	6.7
Total Phytoplankton	153.68	0.00	77.9		313.38	85.2		226.39	41.7	15.20	54.4
Radiolaria	0.76	0.63	0.4		0.38	0.2		0.87	4.5	0.38	1.3
Acantharia	6.25	8.84	3.2		22.50	0.2		10.00	0.4	0.09	0.3
Foraminifera	0.46	0.49	0.2		0.38	0.2		0.35	1.8	0.15	0.5
Tintinnids	5.80	3.19	2.9		3.00	1.8		0.94	4.9	1.46	5.2
Total Protozoa	13.27	0.00	6.7		26.25	2.5		12.17	11.6	2.08	7.4
Copepod eggs	6.60	0.71	3.3		3.08	1.9		2.31	12.0	6.22	22.2
Nauplii	20.34	6.16	10.3		12.00	7.2		5.87	30.5	3.66	13.1
Copepoda	1.66	0.76	0.8		4.25	2.6		0.22	1.2	0.26	0.9
Ostracoda	0.66	0.16	0.3		0.17	0.1		0.24	1.3	0.20	0.7
Pteropoda	0.07	0.10	0.0		0.29	0.2		0.00	0.0	0.22	0.8
Larval Bivalves	0.52	0.47	0.3		0.38	0.2		0.19	1.0	0.02	0.0
Appendicularia	0.37	0.24	0.2		0.29	0.2		0.15	0.8	0.11	0.4
Total Metazoans	23.63		12.0		17.38	10.5		6.67	34.6	4.47	38.2

%AFDW, %C, %N, %P refer to DW. No./m^3 (in thousands) is the average density of any taxa, S.D., standard deviation, % of total, its numerical contribution.

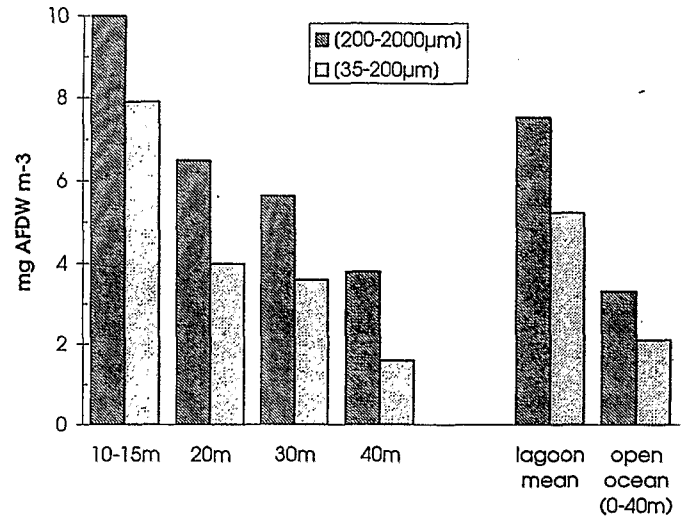

Fig. 7. Mean plankton biomasses with respect to depth. Biomasses refer to ash-free dry weight (AFDW).

7.8% of the DW) are found at the 10–20 m stations. Detritus is also generally found at the shallow stations (up to 32% of total DW).

The [35–200 µm] fraction is dominated by phytoplankton cells, mainly diatoms, so that it cannot be named microzooplankton (Table 7). Therefore, it is not surprising that the AFDW percent contribution to DW is much lower in the 35–200µm size fraction than in the >200 µm fraction (26.7% vs 68.4%) since this percentage is known to be lower in the phytoplankton than in the zooplankton (Lovegrove, 1966; Lenz, 1974). Such a result for AFDW is also observed in the C, N, P composition: the mean percentages of carbon, nitrogen and phosphorus in the small fraction are 20.8%, 3.0% and 0.33% respectively, but 28.9%, 5.5% and 0.70% in the >200 µm size fraction.

3.3.2. Metabolic rates (excretion, respiration, production and ingestion)

The mean excretion rates per day measured at 23.3–23.8°C in the lagoon show that the rates are lower for the small size fraction (Table 8). This result is not unusual, and

Table 8
Mean daily zooplankton excretion rates (µM mg^{-1} $DW \cdot d^{-1}$) measured at 23.3–23.8°C, and excreted amounts (µM $m^{-3} \cdot d^{-1}$) calculated on the 10 stations (28 data sets)

Size-class	Excretion of			
	NH_4	N_{total}	PO_4	P_{total}
Rates				
[35–200 µm]	1.43 (0.72)	2.54 (2.14)	0.15 (0.08)	0.31 (0.25)
[200–2000 µm]	2.12 (1.01)	3.86 (1.65)	0.17 (0.07)	0.43 (0.21)
Amounts				
[35–200 µm]	34.6	61.4	3.5	7.5
[200–2000 µm]	25.5	46.3	2.1	5.2
Total	60.1	107.7	5.6	12.7

Standard deviations in brackets.

Table 9
Mean atomic ratios between respiration (O), inorganic (NH_4 and PO_4) and total (N_{total} and P_{total}) excretions and contribution of inorganic compounds to total excretion

Size-class	O/NH_4	O/PO_4	O/N_{total}	O/P_{total}	NH_4/PO_4	N_{total}/P_{total}	$\%NH_4/N_{total}$	$\%PO_4/P_{total}$
35–200 μm	21.0	29.1	14.7	108	12.1	6.2	69.4	42.9
200–2000 μm	17.9	24.1	10.8	112	12.6	8.4	53.8	43.3

Calculations refer to the whole lagoon.

can be partly explained by a high occurrence in this fraction of organisms which do not excrete N and P as phytoplankton cells, trypton, mollusc larvae or earlier crustacean developmental stages. The daily excreted amounts per m^3, calculated by multiplying the mean excretion rates by the dry weights (Table 8), are slightly higher than the ones reported in Tikehau atoll by Le Borgne et al. (1989): 33, 35.6, 2.9 and 3.8 μM NP m^{-3} d^{-1}, for NH_4, N_{total}, PO_4, P_{total} respectively. Considering the high ratios between respiration (*O*), nitrogen (*N*) and phosphorus (*P*) excretion (*O/N, O/P, N/P,* Table 9), it appears that the catabolism of lipids and carbohydrates is relatively high in the lagoon. On the other hand, the low percentage of inorganic excretion (40% to 70% of the total N and P excretions) indicates the rather low importance of ammonotelic animals in zooplanktonic populations (Le Borgne, 1986). Finally, the relatively low *N/P* excretion ratios suggest a high efficiency of nitrogen utilization by the zooplankton.

The mean production, in terms of N and P (Table 10), is obtained by combining the mean net growth efficiencies for nitrogen and phosphorus ($K_{2,N}$, and $K_{2,P}$) with the excretion amounts (see Section 2). Carbon production, inferred from nitrogen production is 6.3 mg C m^{-3} d^{-1} for the small fraction and 4.1 for the large fraction, thus leading to a total production of 10.4 mg C m^{-3} d^{-1} (Table 10). The calculated *P/B* ratio, equal to 114%, independently of the size-class, corresponds to a turn-over time of 21 h.

Table 10
Zooplankton excretion, production, ingestion ($mg \cdot m^{-3} \cdot d^{-1}$) and biomass ($mg\ m^{-3}$)

Size-class	Total excretion	Net growth efficiency (K_2)	Production	Ingestion	Biomass	P/B (%)
Nitrogen						
35–200 μm	0.86	0.488	0.82	2.40	0.73	113
200–2000 μm	0.65	0.538	0.76	1.69	0.66	114
Phosphorus						
35–200 μm	0.23	0.361	0.13	0.52	0.08	166
200–2000 μm	0.16	0.446	0.13	0.41	0.08	154
Carbon						
35–200 μm			6.32	17.31	5.64	113
200–2000 μm			4.12	12.23	3.60	114

N and P productions are assessed from excretion, using calculated net growth efficiencies (K_2). C production is calculated from N production using the measured C/N mass ratio for microzooplankton (7.72) and mesozooplankton (5.45). N and P ingestion are calculated from excretion and production values using an assimilation efficiency of 0.7. C ingestion is obtained from N ingestion with a measured C/N mass ratio for particles (7.22). Percent contribution of C, N, P to DW are used to calculate zooplankton biomass.

Ingestion is assessed from production data using an average assimilation coefficient for organic matter (D) of 0.7 given by Conover (1966). However, it should be noted that this coefficient is probably higher in atoll ecosystems as shown by Gerber and Gerber (1979) for C and N, and by Le Borgne et al. (1989) for N and P. Ingestion data for N and P may be converted into a carbon ingestion using the particulate C/N mass ratio of 7.22 (Table 10). Adding the ingestion of the <200 μm and >200 μm size-fractions, we obtain an estimate of the mean zooplankton C ingestion of 29.5 mg C m^{-3} d^{-1}.

From the total zooplankton production (10.4 mg C m^{-3} d^{-1}), a potential production can be assessed for zooplanktivorous animals taking the usual 10% efficiency for this transfer. According to the taxonomic data showing a very low contribution of planktonic predators (4.6% in terms of biomass), it can be inferred that fishes and benthic particle-feeders make the bulk of planktivorous animals. Provided their carbon content is ca. 10% of the wet weight, a potential planktivorous production may be calculated as follows: $10.4 \times 0.1 \times 0.1 = 0.104$ mg wet weight m^{-3} d^{-1}, or 1.25 kg of wet weight per ha and per day considering an average lagoon depth of 15 m.

4. Discussion

4.1. Extrapolation of present observations to a longer period

Our observations lead to the main question: how is the situation encountered in September 1992, representative of a longer period of time? Considering primary production is limited by nutrient availability and not by light and temperature, which are favourable all year long, we assume that only temporary and seasonal inputs into the lagoon can change the ecosystem functioning. Let us list and discuss the possible causes of temporal variability in Uvea lagoon. Firstly, the inputs by land drainage are usually weak on low coral islands, compared with high islands of the Pacific (Dandonneau and Charpy, 1985). Therefore, heavy cyclonic rains have a small impact on lagoon enrichment. A second possible input deals with nutrients originating from the surrounding ocean. Since the oceanic mixed layer is typically nutrient-undetectable from the surface down to 80–100 m, an upwelling process is required to bring them to the surface. Yet, no upwelling, linked to an island mass effect, was found in the Loyalty archipelago (Le Borgne et al., 1985). The other nutrient sources are associated with recycling in the sediment and/or endo-upwelling (Rougerie and Wauthy, 1986), but they probably do not follow any temporal variations. At last, a lagoonal Chl *a* enrichment could originate from the surrounding ocean during austral winter, a period of higher surface Chl *a* concentrations in the 20–22°S oceanic region, owing to mixing (Dandonneau and Gohin, 1984). Surprisingly, no surface Chl *a* increase was observed at our oceanic stations, although they were sampled in austral winter. As a result, we speculate that the situation observed during our study does not undergo significant temporal variations, so our results probably refer to a situation representative of a longer time-span.

4.2. Spatial distribution

Water column hydrological characteristics (temperature, salinity, dissolved oxygen) are quite similar inside, and outside, the lagoon. Likewise, dissolved nutrient levels, particularly that of nitrogen, are low or undetectable in both environments. Such an observation on nutrient concentrations may be surprising since significant NO_3, NO_2, NH_4 or PO_4 amounts were recorded in most other atoll lagoons (Sournia and Ricard, 1976; Delesalle and Sournia, 1992; Charpy-Roubaud and Charpy, 1994). In order to minimize the conservation effect, a common problem in nutrient measurements, our analyses were performed immediately on board. The similarity between lagoonal and open ocean waters can be interpreted as being due to important exchanges through the many passes, except in the eastern part. Two other observations are in favour of this conclusion, i.e., the quasi-homogeneity of hydrology throughout the lagoon and the similarity of copepod species inside and outside. Besides, the lack of vertical stratification seems to indicate that mixing, related to wind and combined with shallow depths, is likely to be another efficient process, at least at this period of the year. On the whole, Uvea lagoon is quite different from semi-closed or closed atoll lagoons which have reduced exchanges with the surrounding ocean: the consequences will be seen on the way that the pelagic ecosystem functions and on the biomass levels.

In spite of null nutrient concentrations in both environments, the lagoon contains higher planktonic biomasses than the open ocean, inside/outside ratio being 2. Distribution of phytoplankton (0–10 m) and zooplankton concentrations (per m^3) display a clear positive gradient from deep to shallow depths, leading to a W–E gradient. We believe that higher Chl *a* concentrations in the shallow eastern part simply result from greater microphytobenthos inputs by mixing, in contrast to the western part which is deeper and wide open. Such a combined effect of bathymetry and exchanges with the ocean has already been pointed out by Gordon et al. (1971) and Delesalle and Sournia (1992). Influence of microphytobenthos on observed Chl *a* data is reflected in the dominance of the Chl $a>1$ μm in the lagoon, while the Chl $a<1$ μm exceeds 50% outside in the same nutrient-depletion conditions. Such an effect of microphytobenthos is confirmed by microscopic observations on 35 μm net samples. On the other hand, the zooplankton gradient is probably due to the importance of bottom zooplankton which predominates in shallow depths. This bentho-zooplankton is not caught during the day by vertical hauls as revealed by the high day/night ratio of 49% for mesozooplankton biomasses.

4.3. Plankton biomass and production in the lagoon

Chl *a* and phytoplanktonic cell concentrations in Uvea lagoon are quite similar to those reported in the Great Barrier Reef by Furnas et al. (1990); Ayukai (1992). However, cell counts are far lower than in two atolls of the Tuamotu archipelago: Tikehau (semi-closed atoll), and Takapoto (landlocked atoll). For example, there are 10–30 times less cyanobacteria and 2–10 times less microalgae in Uvea than in Tikehau (Blanchot et al., 1989) and even less compared to Takapoto (19–33, 2–19 respectively, Charpy et al., 1992). Likewise, mean particulate carbon concentration (16 μM C m^{-3}),

found by Charpy and Charpy-Roubaud (1991) in Tikehau, is more than twice as high as in Uvea. In terms of primary production, Uvea appears to be less efficient than the closed atoll of Takapoto, as evidenced by the high dissolved oxygen increase (33%) between sunrise and sunset, observed by Sournia and Ricard (1976), a value to be compared with our 0.3–8% in Uvea. Similarly, Uvea lagoon displays lower zooplankton biomasses than other lagoons. Thus, when zooplankton standing stocks are matched with data obtained with similar methods in other lagoonal environments such as Tikehau atoll (Tuamotu archipelago, French Polynesia) and the SW New Caledonia lagoon (Fig. 8), Uvea displays the lowest mesozooplankton AFDW. Moreover, the contribution of the smaller fraction (35–200 μm) is more important in Uvea (40% vs. 24% in Tikehau), which is also an index of oligotrophy according to the general rule found by Le Borgne and Rodier (in press) for the western Pacific ocean.

Possible reasons for the relatively low biomass and production in the lagoon, include a short residence time of the water due to large exchanges with the oligotrophic surrounding ocean, and a small nutrient flux from the substrate, as indicated by low nutrient levels observed in bottom samples. This bottom effect could be due to benthic recycling as evidenced by Sournia (1977), and/or to an endo-upwelling process (Rougerie and Wauthy, 1986). It is assumed the impact of the bottom on the water column is weak because recycled or endo-upwelled nutrients are taken up primarily by phytobenthos. This assumption is supported by measurements of Clavier et al. (1995) on benthic primary production, which appears to be more than twice as high as the planktonic production (5.3 vs. 2.5 mg C m^{-3} h^{-1}). Interestingly, these authors point out the importance of the microphytobenthic production in Uvea compared with the SW New Caledonia lagoon.

Finally, the abundance of *Trichodesmium*, especially at the shallow stations, put the question of the contribution of molecular nitrogen based production in pelagic lagoonal ecosystems. These organisms have been described as common in coastal and oceanic oligotrophic waters of the Southwestern Pacific (Dupouy, 1992).

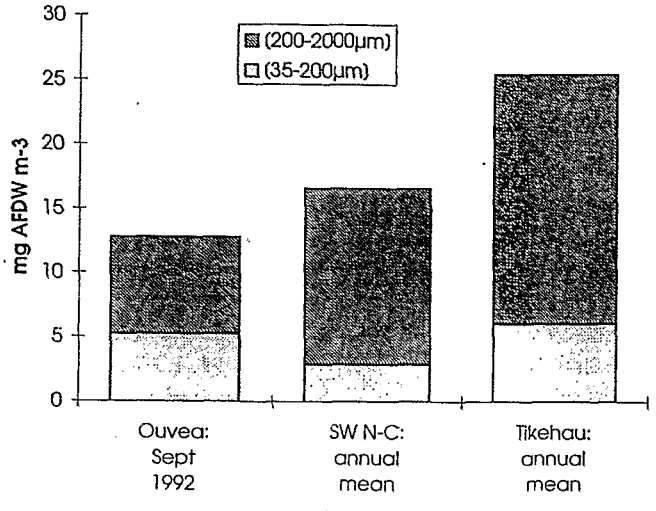

Fig. 8. Comparison between plankton standing crops (mg m^{-3} AFDW) of three lagoons: Uvea, SW New Caledonia (Le Borgne, pers. comm.) and Tikehau (Le Borgne et al., 1989).

4.4. Phytoplankton and zooplankton productivities (P/B) and trophodynamics

In spite of relatively low planktonic biomasses, high productivities (P/B) were found for both phytoplankton and zooplankton. Productivity for phytoplankton is 10.7 g C/g Chl a^{-1} h^{-1}, which is consistent with estimates obtained in the Great Barrier Reef at the same latitude for a similar chlorophyll biomass (9–11 g C/g Chl a^{-1} h^{-1}; Furnas et al., 1990) and in Tikehau atoll (9 g C Chl a^{-1} h^{-1}; Charpy-Roubaud and Charpy, 1994). This hourly productivity in Uvea can be converted into a daily *P/B* of 235%, considering a 11 h light period in September and, using a C/Chl *a* ratio of 50, found by Charpy-Roubaud and Charpy (1994) in Tikehau atoll and by other authors in the tropical ocean (Laws et al., 1987; Chavez et al., 1991). Such a high daily *P/B* is equivalent to a very short turn-over time. For zooplankton, *P/B* is equal to 114%, leading to a 21 h turn-over time, which is relatively short but not uncommon (Le Borgne et al., 1989). High *P/B* values can have a methodological or a natural origin. In the methodological hypothesis, bias could come from, either an overestimation of excretion rates and net growth efficiencies which lead to the production (*P*) term, or an underestimation of C, N, P biomasses (*B*), originating from low percent contributions of these elements to the DW. Because excretion rates and growth efficiencies are in the usual range, the most likely bias could deal with the C, N, *P* percent contributions, which are low (Tables 6 and 7). In the natural hypothesis, high *P/B* and associated short turn-over times appear to be a characteristic of oligotrophic environments and they have long been a paradox for oceanographers. Explanations of such a paradox, are generally found in the size structure and in the floristic and faunistic compositions. In Uvea, like in other oligotrophic environments, dominant primary producers are tiny cells (<1 μm) such as cyanobacteria, which are suspected to function on regenerated nutrients. This minute phytoplankton population is associated with a large proportion of zooplankton species presenting a short turn-over time (e.g., appendicularia, early copepod stages).

The zooplankton community is mostly made of particle-feeders with a carbohydrate–lipid metabolism (as shown by the high *O/N* ratio, Table 9), which indicates its diet is made mainly of phytoplankton and detritus. Although planktonic primary productivity (27.5 mg C m^{-3} d^{-1}) balances zooplankton carbon ingestion (29.5 mg C m^{-3} d^{-1}), suggesting its nutritional needs could theoretically be met by phytoplankton alone, most of zooplankton diet is probably made of detritus as in other coral environments (Gerber and Gerber, 1979; Gottfried and Roman, 1983). Thus, phytoplankton carbon contribution to total carbon is estimated to be 15.5%, when mean Chl *a* and carbon concentrations (0.233 and 75.3, respectively) and a $C/Chl\ a = 50$ ratio are used. In other words, most of the diet of particle-feeders in Uvea would consist in detritus and non autotrophic organisms. The question remains, however, about the possibility for zooplankton to ingest submicronic particles, which make 20–50% of phytoplankton and probably the same for other kinds of particles. In Uvea, significant proportions of pteropods and appendicularians, which have been reported to feed on particles <1 μm (Turner, 1984; Deibel and Lee, 1992), were found together with radiolarians and foraminiferans in the zooplankton. This is in favour of the ingestion of a wide spectrum of particle sizes by zooplankton, among which detritus make a large proportion.

Finally, if we assume an equilibrium between zooplankton production and its

consumption by planktivorous animals, we can calculate a potential production of 1.25 kg per ha and per day. Such a value may be compared with fish production estimate (Clavier et al., 1995) of 0.100 to 0.250 kg per ha and per day: therefore, zooplankton production appears to be consumed also by benthic planktivores, such as bivalves and corals.

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