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Phytoplankton biomass and production in two Tuamotu atoll lagoons (French Polynesia)

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ABSTRACT: Nutrient concentrations, phytoplankton biomass (chlorophyll *a*, chl *a*) and primary production (^{14}C uptake) were measured over a 5 yr period (1990 to 1994) in the atoll lagoons of Takapoto (4 yr water residence time; with pearl oyster aquaculture) and Tikehau (0.5 yr residence time; without pearl oyster but with a fishery), French Polynesia. In both atolls, phosphate and silicate concentrations (0.1 µM PO_4 and 0.8 µM SiO_2) were lower inside the lagoon than in surrounding oceanic surface waters. Picoplankton <1 µm dominated phytoplankton biomass (61%) and productivity (55%) in both lagoons. Average assimilation numbers were high (13 mg C mg^{-1} chl *a* h^{-1}) and average chl *a* doubling rates of the <1 µm fraction were estimated to be 1.1 and 1.3 d^{-1} in Takapoto and Tikehau, respectively. Average daily primary production during the 1991 to 1994 period in Takapoto and Tikehau lagoons was estimated to be 0.8 and 0.7 g C m^{-2} d^{-1}, respectively.

KEY WORDS: Nutrients · Phytoplankton Production · Pearl oyster · Atoll lagoon French Polynesia

INTRODUCTION

Atoll lagoons play an important role in the French Polynesian economy: cultured pearls from pearl oysters cultured in Tuamotu atoll lagoons are French Polynesia's most valuable export. Lagoon productivity studies are necessary to estimate their culture potential. Indeed, the oysters feed only on natural lagoon production and furthermore cannot retain particles <3 µm (Charpy 1994). Primary production of some Polynesian atoll lagoons has been studied since 1974: Takapoto (Sournia & Ricard 1975, 1976), Tikehau (Charpy-Roubaud et al. 1989, Charpy & Charpy-Roubaud 1990a, b), Scilly (Ricard & Delesalle 1981), and Mataiva (Delesalle et al. 1985). Two multidisciplinary programs were launched in 1991 to improve knowledge on Tuamotu lagoonal ecosystems: Programme Général de Recherche sur la Nacre (PGRN) in Takapoto (14° 30' S, 145° 20' W) and CYcle de l'Energie et de la matière dans les Lagons d'atolls (CYEL) (Charpy 1992) in Tikehau (15° 00' S, 148° 10' W). The main objective of the PGRN project was to compare current environmental conditions with conditions existing before aquaculture began there and to study the biology of the pearl oyster *Pinctada margaritifera*. The CYEL program is a continuation of the ATOLL program (1982 to 1988), with a special focus on the pelagic microbial loop. The present study fits into the PGRN and CYEL programs.

Here, we present results from primary production experiments carried out over a 5 yr period (1990 to 1994) in 2 lagoons: Takapoto (a closed atoll) and Tikehau (an atoll with a passage). The experiments were undertaken with 2 goals: (1) to estimate the average productivity of the lagoons, and (2) using size-fractionation methods, to estimate relative contributions of phytoplankton sub-populations to community productivity.

MATERIAL AND METHODS

Study sites. Takapoto is located in the north of the Tuamotu Archipelago. It has a surface area of 74 km^2, of which 23 km^2 is emerged rim and 51 km^2 is lagoon. There is no passage and exchange between ocean and lagoon is by reef flat spillways (10 m wide, 10 cm

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deep). Prevailing winds are from the east. The average depth is 25 m and the average replacement time for water in the lagoon is 4.2 yr (Sournia & Ricard 1976). Pearl culture was begun on a regular basis in 1970.

Tikehau is situated in the northwest of the Tuamotu archipelago; its geomorphological characteristics make it a suitable model of a mid-size open atoll. 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 km^2; of this, 91% has a depth greater than 15 m, while the average depth is 25 m (Lenhardt 1991). The 25 km^2 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 for those in the passage, currents in spillways generally flow into the lagoon at low speed. The average outward flow in the passage is 700 $m^3 s^{-1}$; therefore, a simple average replacement time for waters in the lagoon is 176 d (Lenhardt 1991). Fishery is the main resource of Tikehau inhabitants.

Water sampling. Phytoplankton biomass in Takapoto was sampled monthly between 1990 and 1992 at 3 stations (Stns 1, 2 and 3) (Fig. 1). Primary production measurements were performed monthly between March 1990 and November 1990 at these stations. Measurements were also made during June 1991, September and November 1993, and February and November 1994 at 8 stations (Fig. 1). The Tikehau atoll lagoon was sampled for biomass and primary production measurements 7 times between 1991 and 1994 in January and November 1991, March, May and November 1992, March 1993 and October 1994. Six stations were occupied within the lagoon. One of these stations is the lagoon reference station (Stn 3) discussed earlier (Charpy & Charpy-Roubaud 1991). Two stations (Stns 1 and 2) are located windward and leeward of a reference pinnacle (Charpy & Harmelin-Vivien 1992) to observe how coral pinnacles may influence lagoonal waters. Water samples were collected with acid-cleaned Niskin bottles at the surface and 5 m depth intervals to 25 m.

Primary production measurements. Between 2 and 5 subsamples of unscreened sea water (Furnas 1987) were incubated *in situ* between 10:00 and 14:00 h with 2 µCi of ^{14}C-bicarbonate (added with a plastic-tipped micropipette) in 1000 ml borosilicate glass bottles (1990) or 300 ml polycarbonate bottles (1991 to 1995). Special care was taken after 1990 to avoid exposing the samples to bright light. Three bottles were wrapped in black plastic for dark assimilation estimation. In 1990, following incubation, bottle contents were filtered through 10 µm Nuclepore filters; pressure heads during fractionation never exceeded 0.004 atm. The filtrates were sequentially refiltered onto 2 µm and 0.2 µm Nuclepore filters. One of the bottles was filtered directly through a 0.2 µm Nuclepore filter for estimation of total production. Between 1991 and 1994, incubation bottles were filtered successively through 3 µm and 1 µm Nuclepore filters and then 25 mm Whatman GF/F glass fiber filters. One of the bottles was filtered directly through GF/F filters for an estimate of total production. First results for Takapoto indicated that total production and biomass measured using GF/F filters was equal to production and biomass measured using 0.2 µm Nuclepore filters (Charpy et al. 1992). To remove inorganic carbon 250 µl of 0.5 N HCl were added to the filter in the scintillation vial. Twelve hours later, 100 µl of Protosol was added to the filter. Radioactivity on the filters was measured with a liquid scintillation counter and corrected for quench by using an internal standard and channels ratio method. Carbon

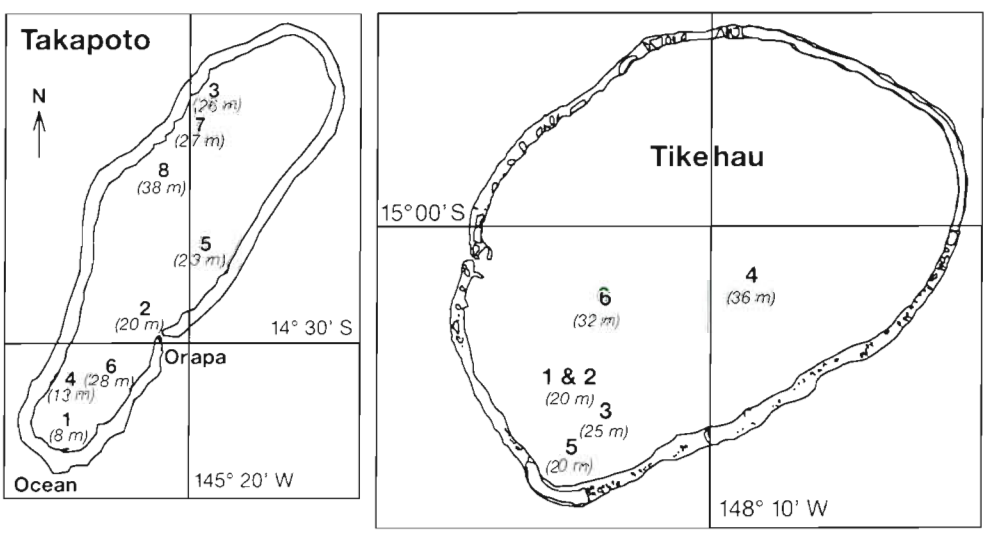

Fig. 1. Locations and depths of stations in Takapoto and Tikehau lagoons (Tuamotu Archipelago)

uptake was calculated using ΣCO_2 = 90 mg l^{-1} for the 1990 data and using the ΣCO_2 calculated from total alkalinity measurements for the 1991 to 1994 data. Areal production was calculated by trapezoidal integration.

Total alkalinity (TA) determinations were performed on acidified sea-water samples by the method of Perez & Fraga (1987). Total alkalinity data were not corrected for changes in nutrient concentration (Chisholm & Gattuso 1991). Carbonate alkalinity (CA) was calculated by the equation: CA (meq l^{-1}) = TA – BA, with BA (borate alkalinity; meq l^{-1}) calculated as:

$$BA = \Sigma B\left[\frac{a_H K_{1b} + 2K_{1b}K_{2b}}{a_H^2 + a_H K_{1b} + 2K_{1b}K_{2b}}\right]$$

where ΣB is total boron (mmol l^{-1}) = 0.01 × salinity; a_H is hydrogen ion activity (10^{-pH}); and K_{1b}, K_{2b} are the first and second dissociation constants for boric acid. Values for these constants are tabulated as functions of temperature and salinity in Riley & Skirrow (1975).

Total CO_2 (ΣCO_2) was calculated from the equation:

$$\Sigma CO_2 = CA\left[\frac{K_{1c}a_H + K_{1c}K_{2c} + a_H^2}{K_{1c}a_H + 2K_{1c}K_{2c}}\right]$$

where K_{1c}, K_{2c} are the first and second dissociation constants for carbonic acid (Riley & Skirrow 1975).

Chl *a* determination. Chl *a* concentrations were determined by fluorometry (Yentsch & Menzel 1963). For chl *a* determinations, 250 ml of water sample were size fractionated by the same methods as productivity samples: they were successively filtered through 3 µm and 1 µm Nuclepore filters and finally through a GF/F (Whatman) filter Pressure heads during fractionation never exceeded 0.004 atm. Fluorescence was measured before and after acidification with 50 µl of 1 N HCl. The fluorometer was calibrated using a Sigma chl *a* standard.

Environmental data. Water temperature and salinity measurements were obtained with a Hydrolab sensor

Dissolved nutrient [NH_4, NO_2, NO_3, $Si(OH_4)$, PO_4] concentrations were determined shortly after sampling in a field laboratory using the standard techniques described by Strickland & Parsons (1972). Surface irradiance was recorded during incubations with a Li-Cor solarimeter, and daily production estimated by dividing the production measured during the incubation period by the fraction of total daily irradiance during that period or, in case of a lack of light energy data, by multiplying hourly production by 10.

RESULTS

Environmental characteristics affecting phytoplankton productivity. In Takapoto, lagoonal water temperature varied between 27°C during the dry season (July to September) and 30°C during the months of March and April, with an average of 29.0°C. Salinity varied between 37 and 39.5 psu, depending on the precipitation, with an average of 38.2 psu. In Tikehau, lagoon water temperatures were similar (average 28.5°C, Charpy 1985) but salinity was lower (35.5 psu, Charpy 1985). We have no precipitation (P) or evaporation (E) data for Takapoto or Tikehau, but Magner & Wauthy (1976) estimated that E – P = 0.5 m yr^{-1} in Takapoto. The evaporation-precipitation budget is probably the same in Takapoto and Tikehau and the difference in salinity reflects different lagoon-ocean exchanges.

Nutrient concentrations measured in Takapoto and Tikehau lagoons are summarized in Table 1. In November and February, ammonium and nitrate concentrations in Takapoto lagoon were generally <0.2 µM, except at Stn 1, located close to the village, where concentrations up to 0.25 and 0.4 µM, respectively, were measured. No difference was noted relative to surface oceanic waters. Phosphate and silicate concentrations in the Takapoto lagoon were <0.05 and 0.5 µM, respectively. These levels are one-half to one-quarter of those in surface oceanic water (Fig. 2). Registered daily insolation (PAR) varied from 21 E m^{-2} d^{-1} in May to 53 E m^{-2} d^{-1} in September and February. Underwater light levels at 25 m (average depth of the lagoon) averaged 7.4 % of surface irradiance.

In Tikehau, PO_4 and NH_4 concentrations were 2 times and 6 times higher, respectively, than in Takapoto. Incident light energy at Tikehau varied between 30 and 60 E m^{-2} d^{-1} (Fig 3), and 17 % of the surface energy reached 25 m (average lagoon depth).

Table 1. Average ± SE nutrient concentrations (µM) in Takapoto (November and February) and Tikehau (January and March) lagoons

Atoll	PO_4	NO_2	NO_3	NH_4	SiO_2
Takapoto	0.07 ± 0.012 (n = 44)	0.05 ± 0.005 (n = 35)	0.19 ± 0.023 (n = 44)	0.19 ± 0.012 (n = 44)	0.53 ± 0.044 (n = 22)
Tikehau	0.14 ± 0.006 (n = 351)	0.02 ± 0.001 (n = 309)	0.07 ± 0.006 (n = 313)	1.26 ± 0.099 (n = 225)	0.83 ± 0.025 (n = 249)

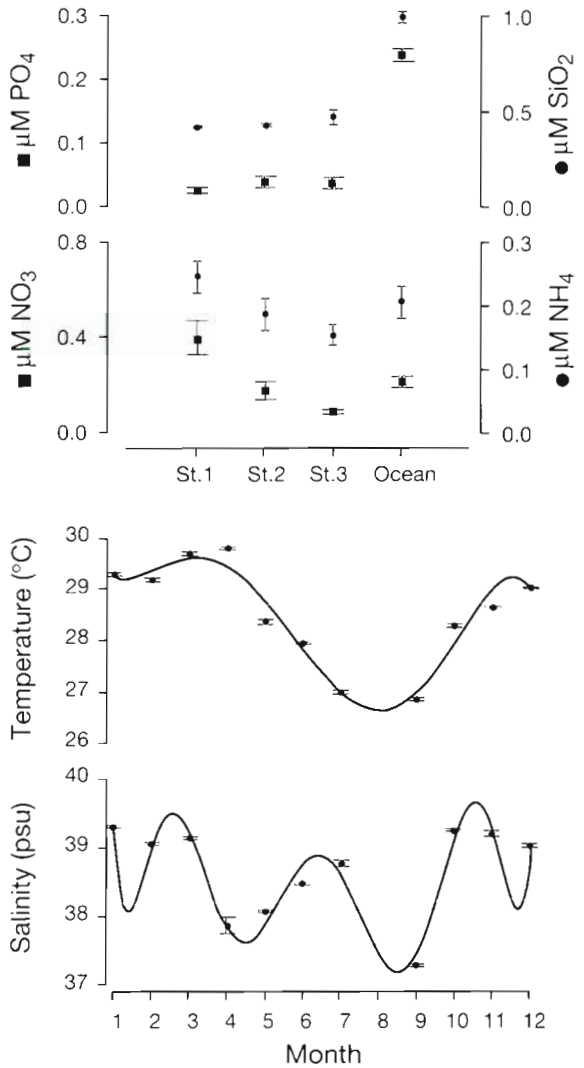

Fig. 2. Average (± SE) dissolved inorganic nutrient concentrations at 3 stations in Takapoto lagoon and one station located in surrounding surface oceanic waters (Ocean), and monthly averages (± SE) of temperature and salinity between 1991 and 1993

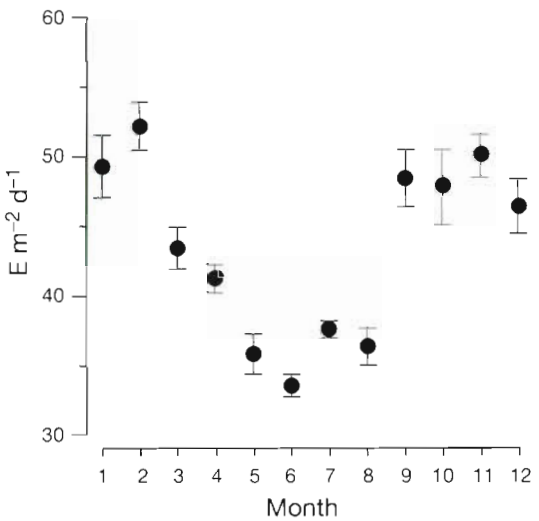

Fig. 3. Monthly average of incident light energy in Tikehau (1991)

Parameters of C uptake measurements. The average ΣCO_2 concentration measured at the beginning of the experiments was 88.2 ± 0.2 mg l^{-1} (n = 39). Dark assimilation never exceeded 10% of the light uptake, and variability of C uptake among 3 sub-samples per depth was <12% of their average.

Comparison between total production and biomass estimated by direct filtration and by the sum of the size class fractions (Takapoto). The integrated production of the 3 size fractions (>10 µm + 10–2 µm + 2–0.2 µm) was highly correlated with the production estimated from direct filtration through a 0.2 µm filter (Fig. 4). A similar pattern was observed between primary production and the chlorophyll biomass where the sum of the size fractions (>3 µm + 3–1 µm +

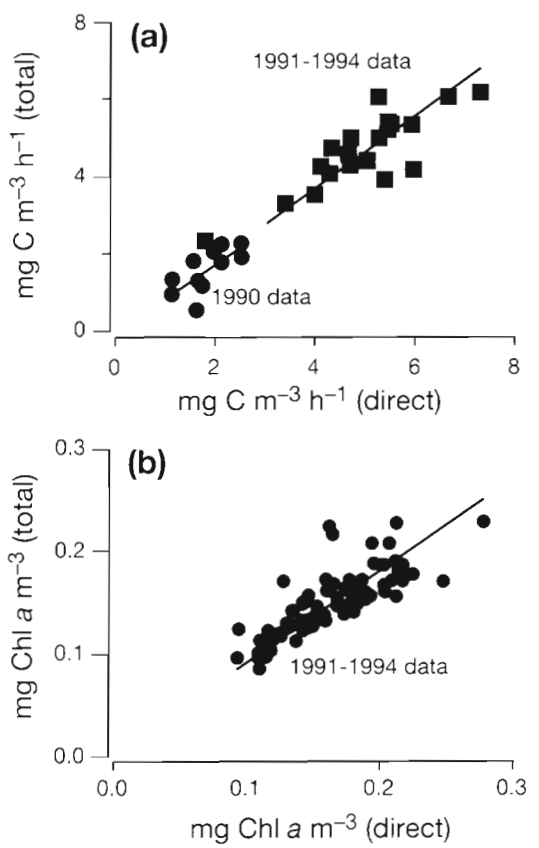

Fig. 4. Comparisons of direct filtration onto 0.2 µm (1990 data) and GF/F filters (1991 to 1994 data) with total filtration: >10 µm + 10–2 µm + 2–0.2 µm (1990) and >3 µm + 3–1 µm + 1 µm–GF/F (1991 to 1994) for (a) primary production and (b) chl *a*. Lines are linear regressions

1 µm–GF/F) was not statistically different from the biomass and production estimated from direct filtration through a GF/F filter.

Vertical distributions of biomass and productivity. With 2 exceptions (profiles 04/90 and 10/90b), vertical profiles of chlorophyll and photosynthesis measured in Takapoto in 1990 (Fig. 5) had photosynthesis maxima at 10 m depth. Maximal photosynthesis rates were consistently <3 mg C m^{-3} h^{-1}. In 1991 to 1994, however, 2 different situations could be observed in the Takapoto lagoon (Fig. 6). Under windy conditions (the most common), phytoplankton biomass was evenly distributed in the water column and exhibited production maxima in the upper 10 m (profiles 06/91 to 02/94c). Under calm conditions (November 1994), biomass and production maxima were found between 15 and 25 m (profiles 11/94a to 11/94d). Maximum photosynthesis rates up to 6 mg C m^{-3} h^{-1} were recorded. In most cases, photosynthesis and biomass profiles exhibited the same trend. Maximum integrated photosynthesis was not correlated with maximum incident light energy. For example, average light energy received at the surface during the June 1991 incubation (06/91) was 3.8 E m^{-2} h^{-1} and the integrated production (upper 25 m) was 0.8 g C m^{-2} d^{-1}; in February 1994 (02/94b), light energy was 7.8 E m^{-2} h^{-1} and integrated production was 0.5 g C m^{-2} d^{-1}.

In Tikehau, representative vertical profiles of chlorophyll and photosynthesis measured between 1991 and 1994 (Fig. 7) showed a uniform distribution of phytoplankton biomass in the water column and a production maximum in the upper 10 m. Maximum photosynthesis rates in profiles up to 6 mg C m^{-3} h^{-1} were consistently measured.

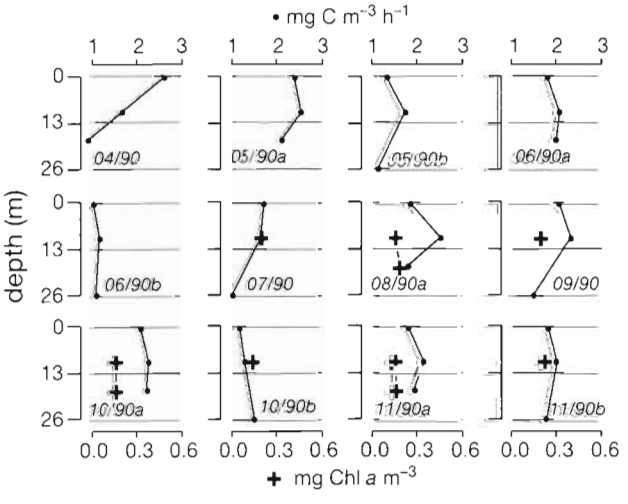

Fig. 5. Vertical profiles of carbon assimilation and chl *a* concentration in Takapoto in 1990. Example of nomenclature: *05/90a* = May 1990 first profile

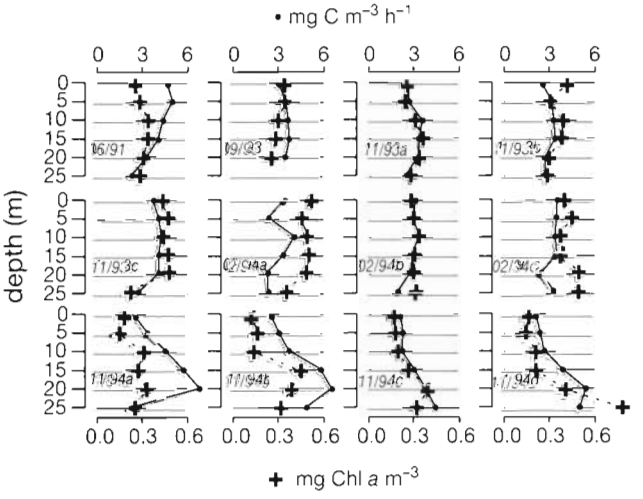

Fig. 6. Vertical profiles of carbon assimilation and chl *a* concentration in Takapoto between 1991 and 1994. Nomenclature as in Fig. 5

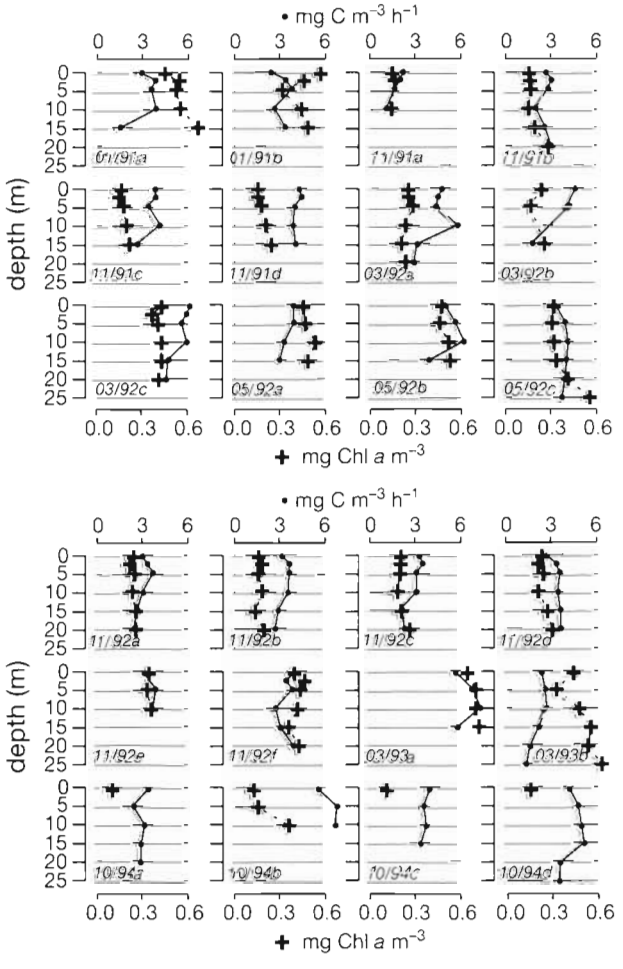

Fig. 7. Vertical profiles of carbon assimilation and chl *a* concentration in Tikehau between 1991 and 1994. Nomenclature as in Fig. 5

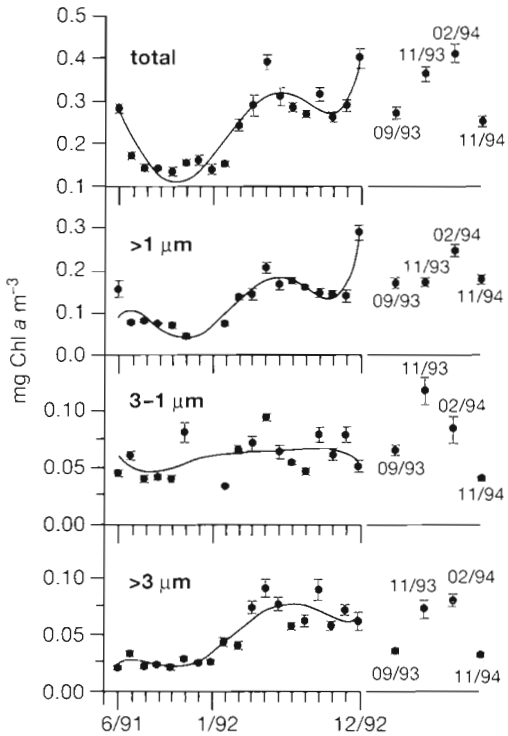

Fig. 8. Monthly average (± SE) of size-fractionated chl *a* in the 1991 to 1994 period in Takapoto. Example of nomenclature: 06/91 = June 1991

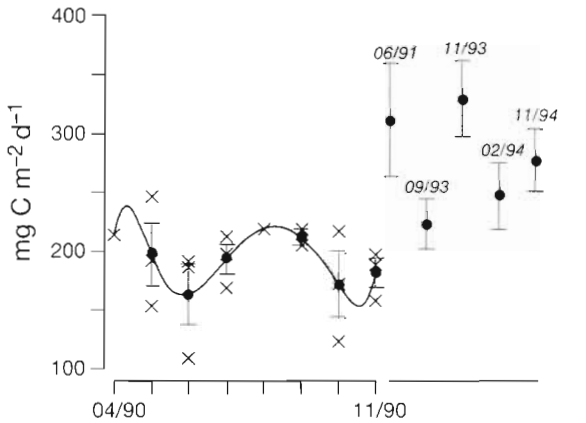

Fig. 9. Seasonal levels (×) and average values (●) ±SE of integrated primary production (upper 10 m) in Takapoto. Values measured during the 1990 time series are connected for visual continuity. Nomenclature as in Fig. 8

Seasonal productivity. Differences in phytoplankton biomass were observed in Takapoto lagoon between 1991 and 1994 (Fig. 8), mostly in the <1 µm and >3 µm size fractions. No significant change in standing crop levels of the 3–1 µm size fraction was observed. Chl *a* concentration was very low between July 1991 and February 1992, with monthly averages <0.2 mg chl *a* m^{-3} The highest daily (upper 10 m) production rates (250 to 450 mg C m^{-2} d^{-1}) were observed in June 1991 and November 1993 in Takapoto (Fig. 9).

Size structure. Phytoplankton size structure was investigated in both Takapoto and Tikehau lagoons. Small phytoplankton dominated standing crop and primary production in both lagoons, regardless of season or depth. Contributions of the <3 µm fraction to primary production and biomass in the 2 lagoons (Table 2) were similar (80 and 82% for primary production and 81 and 78% for chl *a* standing crop). Phytoplankton in the <1 µm fractions in Takapoto and Tikehau lagoons contributed, respectively, 53 and 58% of primary production and 63 and 60% of chl *a* standing crop. During 1990 experiments in Takapoto, phytoplankton >10 µm, 10–2 µm and <2 µm contributed 5.3 ± 0.4%, 20.8 ± 0.9% and 73.9 ± 1.0%, respectively, of total inorganic carbon uptake (n = 36).

Assimilation numbers. In Takapoto and Tikehau lagoons, assimilation numbers (P^B; mg C mg^{-1} chl *a* h^{-1}) in size-fractionated samples varied with depth and size (Fig. 10). Maximum P^B values in all size fractions were measured at 5 m depth, equivalent to 30% of irradiance levels.

Table 2. Percent contributions (mean ± SE) of different size fractions to primary production and chl *a* standing crop in lagoons during ^{14}C uptake measurements

	^{14}C uptake				Chl *a*			
	>10 µm	10–2 µm	<2 µm	<10 µm				
Takapoto 1990	5.3 ± 0.4 (n = 36)	20.8 ± 0.9 (n = 36)	73.9 ± 1.0 (n = 36)	94.7 ± 0.7 (n = 36)				
	>3 µm	3–1 µm	<1 µm	<3 µm	>3 µm	3–1 µm	<1 µm	<3 µm
Takapoto 1991–1994	19.9 ± 0.7 (n = 108)	27.0 ± 0.7 (n = 90)	52.8 ± 1.0 (n = 90)	80.1 ± 0.7 (n = 108)	19.2 ± 0.4 (n = 386)	23.0 ± 0.5 (n = 386)	57.6 ± 0.4 (n = 386)	80.8 ± 0.5 (n = 386)
Tikehau 1991–1994	18.3 ± 0.7 (n = 131)	23.3 ± 0.5 (n = 121)	58.3 ± 0.8 (n = 121)	81.7 ± 0.7 (n = 131)	22.4 ± 0.9 (n = 123)	17.4 ± 0.5 (n = 113)	60.1 ± 0.9 (n = 113)	77.6 ± 0.9 (n = 123)

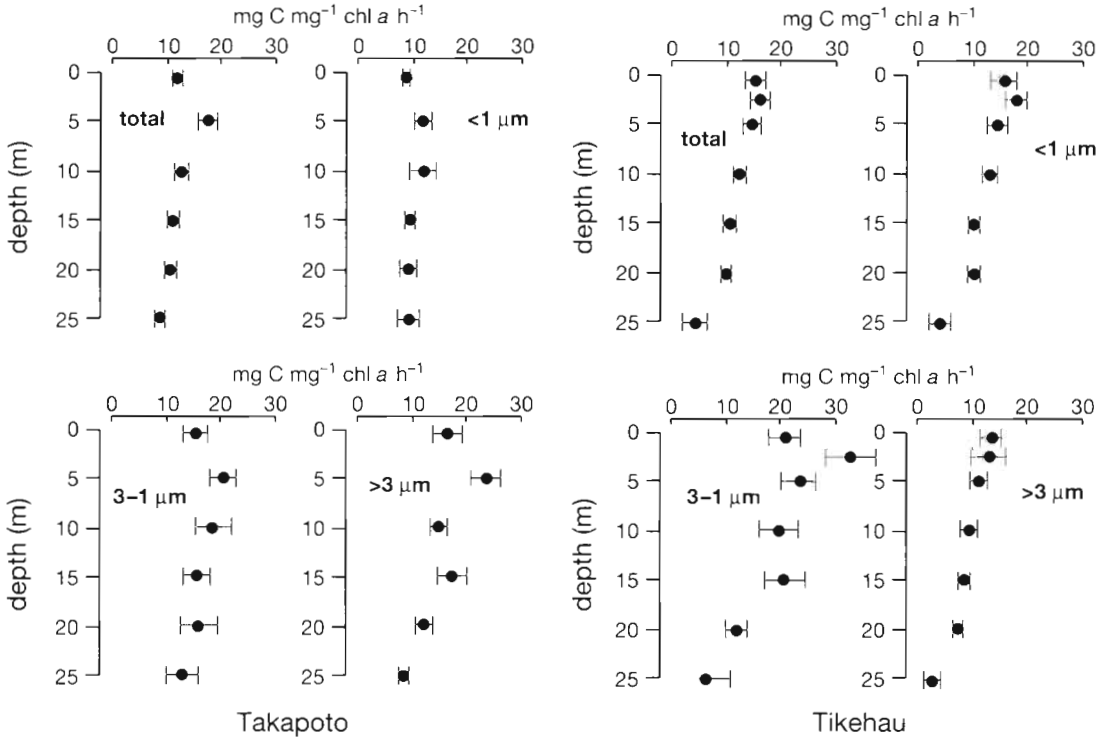

Fig. 10. Average (± SE) vertical profiles of size-fractionated assimilation numbers between 1991 and 1994 in Takapoto and Tikehau lagoons

DISCUSSION

The slight increase in dissolved mineral nitrogen close to the village might reflect the contamination of lagoonal water by sewage.

As in Takapoto lagoon, phosphate and silicate concentrations in Tikehau were lower (0.1 and 0.8 µM respectively) than in surface oceanic water (0.4 and 1.0 µM, respectively, Charpy-Roubaud et al. 1990). Depletion of reactive phosphorus and silicate concentrations in atoll lagoons below oceanic levels has been observed at a number of sites: in Canton Atoll lagoon (Smith & Jokiel 1975), in Christmas Island lagoon (Smith et al. 1984) and in Takapoto atoll (Sournia & Ricard 1976). Large quantities of nitrogen-fixing cyanobacteria inside atoll lagoons may be responsible for the P uptake (Charpy-Roubaud et al. 1996).

The very low level of chl *a* observed in Takapoto between July 1991 and February 1992 is difficult to explain. A spectacular bloom of small jellyfish *Linuche unguiculata* was observed during this period, but we do not know if there is a relation between this bloom and the low phytoplankton biomass. In Tikehau lagoon, proliferation of salps *Thalia democratica* had been observed in April 1985; their ingestion rate was 9 mg C m^{-3} d^{-1}, i.e. 50% of the C uptake by the phytoplankton (Le Borgne et al. 1989). Eleven surveys performed in Tikehau between 1983 and 1985 showed that large differences in chl *a* concentration were independent of season (Charpy & Charpy-Roubaud 1991).

The 1991 to 1994 production rate in Takapoto was significantly higher than that of 1990. Critical examinations of the ^{14}C uptake method (Fitzwater et al. 1982, Marra & Heinemann 1984, Chavez & Barber 1987) have shown that the choice of water sampling and incubation techniques may lead to significant differences in measured primary production rates. This was not appreciated in 1990, while between 1991 and 1994 considerable care was taken to maximize procedural cleanliness and process water samples in a clean manner using polycarbonate incubation bottles. An estimate of average lagoon production can be calculated by integrating the 25 m (average lagoon depth) profile experiments. If we consider only the 1991 to 1994 period for annual primary production estimation, daily primary production values in Takapoto ranged between 0.4 and 1.2 g C m^{-2} d^{-1} with an average of 0.8 ± 0.1 g C m^{-2} d^{-1}. In Tikehau, daily primary production values ranged between 0.4 and 1.1 g C m^{-2} d^{-1} with an average of 0.7 ± 0.1 g C m^{-2} d^{-1}. Therefore, annual production for Takapoto and Tikehau can be estimated respectively to be 292 and 250 g C m^{-2}.

Daily phytoplankton production estimates for Takapoto and Tikehau lagoons fall in the upper end of the

Table 3. Values for phytoplankton community daily production in atoll lagoons. In part from Sorokin (1990)

Location	g C m^{-2} d^{-1}	Source
Rongelap atoll (Marshall Islands)	0.2	Sargent & Austin (1949)
Eniwetok atoll (Marshall Islands)	0.03	Sargent & Austin (1954)
Fanning atoll (Line Islands)	0.1	Gordon et al. (1971)
Ngellelevu atoll (Fiji)	0.01–0.03	Sorokin (1979)
Tarawa atoll (Kiribati)	0.03–0.5	Sorokin (1971)
Butaritari atoll (Kiribati)	0.02–0.30	Sorokin (1971)
Majuro atoll (Marshall Islands)	0.01–0.40	Sorokin (1973a)
Ninigo atoll (Admiralty Islands)	0.16–0.72	Sorokin (1973b)
Sinton atoll (South China Sea)	0.02–0.60	Sorokin & Tyapkin (1984)
Spratly Is. (South China Sea)	0.02–0.20	Sorokin & Tyapkin (1984)
Scott Reef (Timor Sea)	0.01–0.20	Sorokin (1979)
Coetivy Is. (Seychelles)	0.02–0.24	Sorokin & Tyapkin (1984)
Curtaun Reef (Caribbean Sea)	0.01–0.05	Milliman & Mahnken (1972)
Cayos de Albuquerque (Caribbean Sea)	0.01–0.10	Milliman & Mahnken (1972)
Laccadives atoll	0.02–0.09	Quasim et al. (1972)
Scilly atoll (French Polynesia)	0.4	Ricard & Delesalle (1981)
Takapoto atoll	0.4	Sournia & Ricard (1976)
Mataiva atoll (French Polynesia)	0.18–0.72	Delesalle et al. (1985)
Tikehau (1983–1987)	0.44	Charpy-Roubaud et al. (1989)
Rangiroa atoll (French Polynesia)	0.45	Charpy (unpubl.)
Toau atoll (French Polynesia)	0.1	Charpy (unpubl.)
Takapoto (1991–1994)	0.8	This study
Tikehau (1991–1994)	0.7	This study

range of phytoplankton production recorded in atoll lagoon ecosystems (Table 3). However, the majority of the results summarized in Table 3 were not obtained with clean procedures. These new estimations of primary production in Takapoto and Tikehau lagoons are 2 times higher than estimates given by Sournia & Ricard (1975) and Charpy-Roubaud et al. (1989).

The relationship between light and primary production in Takapoto seems to be different from that which we would have expected from the light-primary production model constructed for Tikehau lagoon by Charpy & Charpy-Roubaud (1990a). Phytoplankton physiological state or grazing effect during the incubations may explain the difference.

Phytoplankton production rates in the lagoon varied without discernible seasonality as also observed by Furnas & Mitchell (1987) in outer-shelf waters of the central Great Barrier Reef.

Plankton <1 µm were the dominant size fraction of Takapoto and Tikehau lagoon phytoplankton populations in biomass (63 and 60%) and production (53 and 58%).

Sieburth et al. (1978) considered that the picoplankton is composed of organisms with a size <2 µm. We can estimate the contribution of these organisms to the primary production in Takapoto using 1990 data: the picoplankton (<2 µm) contributed 74% of the phytoplankton production. This value is slightly higher than those given by Furnas et al. (1990) for lagoons of the central Great Barrier Reef (47 to 69%).

The average P^B of the fractions collected by GF/F filters were very close in Takapoto (13.0 ± 0.6; n = 108) and Tikehau (13.3 ± 0.7; n = 126) (Table 4). The ranges of assimilation numbers observed in both lagoons were very high and indicate that phytoplankton were growing at high rates. Such P^B values are commonly measured in subtropical intrusive systems (Yoder et al. 1985), upwelling zones (Malone 1980), coastal waters (Harrison & Platt 1980), and other atolls or close to Pacific islands (Gordon et al. 1971, Sournia & Ricard 1976, Ricard & Delesalle 1981, Delesalle et al. 1985, Legendre et al. 1988).

Community carbon doubling rates per day (μ) were estimated from the P^B per day and the C/chl *a* ratio of the phytoplankton by the equation of Eppley (1972):

$$\mu = \log_2\left(\frac{\text{C/chl } a + P^B}{\text{C/chl } a}\right)$$

Phytoplankton in Takapoto and Tikehau are dominated by *Synechococcus* (Blanchot et al. 1989, Charpy et al. 1992, Charpy & Blanchot 1996). Therefore, we use the *Synechococcus* C/chl *a* ratio of 82 calculated for Takapoto by Charpy et al. (1992) using a C/volume ratio of 0.4 pg C μm^{-3} and an average cell diameter of

Table 4. Average ± SE assimilation number (P^B; mg C mg^{-1} chl *a* h^{-1}) and doubling rate per day (μ) of different size fractions

Lagoon	P^B				μ (d^{-1})		
	>3 µm	3–1 µm	<1 µm	Total	>3 µm	3–1 µm	<1 µm
Takapoto	16.9 ± 1.1 (n = 93)	17.0 ± 1.1 (n = 89)	10.5 ± 0.6 (n = 89)	13.0 ± 0.6 (n = 108)	1.51 ± 0.05 (n = 93)	1.50 ± 0.06 (n = 89)	1.13 ± 0.04 (n = 89)
Tikehau	10.7 ± 0.8 (n = 126)	21.2 ± 1.5 (n = 111)	13.5 ± 0.8 (n = 113)	13.3 ± 0.7 (n = 126)	1.22 ± 0.06 (n = 114)	1.69 ± 0.07 (n = 113)	1.32 ± 0.05 (n = 113)

Table 5. Summary of Takapoto and Tikehau lagoon characteristics during the 1991 to 1994 period. A: lagoon area (km^2); AD: average depth (m); S: salinity (psu); T: temperature (°C); RT: residence time (yr); PO_4: phosphate concentration (µM); Chl *a*: chlorophyll *a* concentration (mg m^{-3}); PP: primary production (g C m^{-2} d^{-1}); $\mu_{<1\ \mu m}$: doubling rate per day of the <1 µm fraction

Lagoon	A	AD	S	T	RT	PO_4	Chl a	PP	Chl *a* < 3 µm	Chl *a* < 1 µm	$\mu_{<1\ \mu m}$
Takapoto	80	25	38.2	29.0	6[a]	0.1	0.27	0.8	81%	58%	1.13 d^{-1}
Tikehau	400	25	35.5	28.5	0.5[b]	0.2	0.32	0.7	78%	60%	1.32 d^{-1}

[a]Sournia & Ricard (1976); [b]Lenhardt (1988)

0.8 µm. Mean carbon doubling rates in different size classes are summarized in Table 4. All size fractions exhibited rapid division rates with averages in the range 1.13 to 1.69 d^{-1}. However, the >1 µm fractions, which had the shortest generation times (0.6 to 0.7 d), consist of microalgae and *Synechococcus* doublet cells, and the C/chl *a* ratio of 82 calculated for *Synechococcus* cannot be applied here. Therefore, we will consider only that <1 µm fraction which was numerically dominated by *Synechococcus*. Average doubling rates for this fraction were significantly different in Takapoto (1.13 ± 0.04 d^{-1}) and Tikehau (1.32 ± 0.05 d^{-1}). These values are high, but lower than the maximal doubling rate of chl (μ_{max} = 1.6 d^{-1}) measured in the tropical shelf waters of the Great Barrier Reef by Furnas (1991).

Takapoto and Tikehau lagoon characteristics are summarized in Table 5. In spite of a large difference in the residence times of the 2 lagoon systems (4 yr for Takapoto and 0.5 yr for Tikehau), phytoplankton biomass and productivity were quite similar. The linear relationship between residence time and phytoplankton biomass expressed as chlorophyll concentrations observed in some French Polynesia lagoons by Delesalle & Sournia (1992) cannot be applied for production. However, these authors consider that such a relationship may not be applicable for residence times longer than 50 d.

CONCLUSIONS

Takapoto and Tikehau atoll lagoons are characterized by low nutrient levels, low phytoplankton biomass, but high biomass-specific productivity. The dominance of picoplankton in biomass (80% >3 µm) and production (60% <1 µm) is probably a characteristic of Tuamotu atoll lagoons. The dominant fraction (<1 µm) grew 1.2 times faster in Tikehau than in Takapoto. Average daily primary production rates were estimated to be 0.8 and 0.7 g C m^{-2}, respectively. However, the relatively low biomass of phytoplankton and its small size has to be taken into account when estimating the capacity of these lagoons to support an extensive aquaculture.

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