Aquat. Living Resour. 14 (2001) 175–182

S0990744000010986/FLA

The phytoplankton of Takapoto Atoll (Tuamotu Archipelago, French Polynesia): time and space variability of biomass, primary production and composition over 24 years

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Received 3 February 2000; accepted 23 October 2000

Abstract − The characteristics of the phytoplankton of Takapoto Atoll are reviewed from the studies conducted between 1974 and 1998. These studies mainly concerned the biomass and primary production of phytoplankton while the taxonomic composition received far less attention. The mean biomass is 0.2–0.3 µg chl $a \cdot L^{-1}$. The phytoplankton is homogeneously distributed on a year scale although an higher biomass (0.8 µg chl $a \cdot L^{-1}$) may temporarily exist in the south part of the atoll under moderate tradewinds or calm weather. The gross primary production reached 0.8 g $C \cdot m^{-2} \cdot day^{-1}$ whereas the net primary production is estimated to be 0.7 g $C \cdot m^{-2} \cdot day^{-1}$. No significant long-term changes of the biomass or primary production can be observed. The implications of this stability are discussed in the context of the mother-of-pearl mariculture. Size fractionated samples revealed the predominance of picophytoplankton which represented more than 60% of the phytoplankton biomass and achieved > 50% of the primary production. The taxonomic composition observed in 1974 showed the predominance of three algal groups: diatoms, dinoflagellates and coccolithophorids. The diatoms were the most diversified group, while the dinoflagellates were the most abundant. No further examination of the phytoplankton was undertaken until 1996. At that time, the microplankton was quite absent, and the phytoplankton communities were dominated by the pico- and nanophytoplankton, mainly chlorophytes, prymnesiophytes and dinoflagellates. This drastic shift of the phytoplankton communities towards smaller size is not clearly understood. It emphasises the need of taxonomic studies for a better understanding of the lagoon ecology. © 2001 Ifremer/CNRS/INRA/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

phytoplankton / taxonomy / pearl oyster / French Polynesia

Résumé − Le phytoplancton de l'atoll de Takapoto (archipel des Tuamotu, Polynésie française) : variabilité spatiale et temporelle de la biomasse, la production primaire et la composition sur une période de 24 ans. Les caractéristiques du phytoplancton de l'atoll de Takapoto sont analysées à partir des études menées entre 1974 et 1998. Ces études ont principalement porté sur la biomasse et la production primaire du phytoplancton tandis que sa composition a reçu une attention bien moindre. La biomasse moyenne est de 0,2–0,3 µg chl $a \cdot L^{-1}$. Le phytoplancton est réparti de façon homogène à l'échelle annuelle bien qu'une plus forte biomasse (0,8 µg chl $a \cdot L^{-1}$) puisse temporairement apparaître dans la partie sud de l'atoll en cas d'alizés modérés ou de temps calme. La production primaire brute atteint 0,8 g $C \cdot m^{-2} \cdot jour^{-1}$ tandis que la production nette est estimée à 0,7 g $C \cdot m^{-2} \cdot jour^{-1}$. Aucun changement significatif de la biomasse et de la production primaire n'est observé sur le long terme. Les implications de cette stabilité sont discutées dans le contexte de l'aquaculture de l'huître perlière. Les prélèvements fractionnés par classe de taille révèlent la prédominance du picoplancton qui représente plus de 60% de la biomasse du phytoplancton et réalise plus de 50% de la production primaire. La composition taxonomique montrait en 1974 la prédominance de 3 groupes d'algues : les diatomées, les dinoflagellés et les coccolithophoridés. Les diatomées étaient les plus diversifiées tandis que les dinoflagellés étaient les plus abondants. Il n'y a pas eu d'autres observations du phytoplancton jusqu'en 1996. A ce moment, le microphytoplancton était pratiquement absent et les communautés phytoplanctoniques étaient dominées par le pico- et le nanoplancton, principalement les chlorophycées, les prymnésiophycées et les dinoflagellés. Les raisons de ce changement drastique de la composition du phytoplancton vers les petites tailles ne sont pas réellement connues. Cette modification souligne la nécessité d'études taxonomiques pour une meilleure compréhension de l'écologie lagonaire. © 2001 Ifremer/CNRS/INRA/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

phytoplancton / taxonomie / huître perlière / Polynésie française

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1. INTRODUCTION

Since the 1970, the mariculture of the pearl oyster *Pinctada margaritifera* (Linné, 1758) was developed in the atoll lagoons of French Polynesia. It induced scientific researches in the framework, firstly, of the UNESCO Man and Biosphere program (Salvat, 1976), then, from 1991 to 1998, of a multidisciplinary research program on pearl oysters (‘*Programme général de recherche sur la nacre*’, hereafter referred to as PGRN). These researches were mainly focused on Takapoto Atoll (Tuamotu Archipelago). In several domains including the phytoplankton, scientific data spread over 24 years, i.e. a quite unique duration in coral reef environments and Takapoto Atoll can be considered as one of the best known atoll in the world.

In atoll lagoons, the primary production – only entry of organic matter in an ecosystem – is mainly achieved by phytoplankton, which exceeds by far the benthic production (Charpy-Roubaud, 1988). Consequently, the characteristics of the phytoplankton communities, i.e. its biomass, primary production and taxonomic composition, are key factors for the success of the pear-oyster farming. Pioneer studies on Takapoto Atoll phytoplankton were undertaken by Sournia and Ricard in August 1974 and 1975, with additional surveys in 1977 and 1978.

The aim of this paper is to review the researches undertaken on phytoplankton since 1974 in Takapoto Atoll. This review attempts to determine the main characteristics of the phytoplankton biomass and primary production, and their spatial and temporal variations, in order to provide mean values to be used in the model of the trophic capacity of the lagoon. The taxonomic composition is also considered.

2. MATERIAL AND METHODS

Takapoto Atoll (145°10 W, 14°40 S) (*figure 1*) is located in the northwestern part of the 75-atoll Tuamotu Archipelago. The lagoon has a surface of 81 km^2 (Andréfouët, 1998) and a mean depth of 23 m (Ricard et al., 1979). It is isolated from the ocean by an almost continuous reef rim without any pass. During high swells and/or strong winds, oceanic waters enter the lagoon through reef-flat spillways (less than 50 cm depth) mostly situated on the northeastern part of the atoll. The residence time of water in the lagoon was estimated to be 4.2 years (Sournia and Ricard, 1976). Because tides and swell are negligible inside the lagoon, wind is the factor that determines water motion, with eastern tradewinds providing the dominant forcing (Rougerie, 1979).

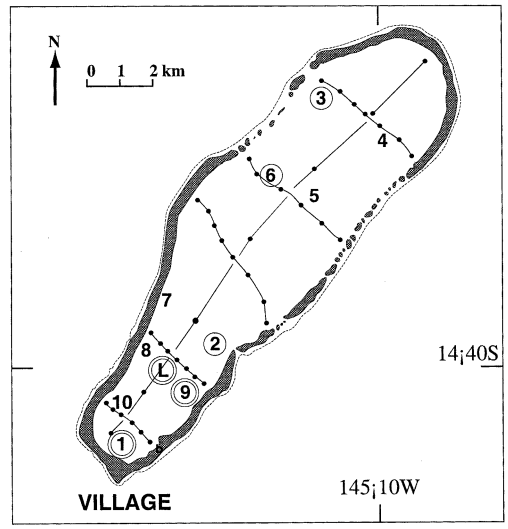

Figure 1. Map of Takapoto Atoll with location of the sampling stations. The following symbols were used to distinguish the various field trips: black dots, Sournia and Ricard (1976) in 1974; numbers, Buestel and Pouvreau (2000) in 1990–1991 and the following studies; encircled numbers, Sakka (1999) in 1996–1997, twice encircled numbers, Loret (1999) in 1996–1997.

2.1. Sampling stations

The studies undertaken on the phytoplankton of Takapoto Atoll are presented in *table I* with the indication of the parameters measured in each study. Positions of the sampling stations are located on *figure 1*.

During the 1974–1979 studies (e.g. Sournia and Ricard, 1975a,b; 1976), the phytoplankton biomass

Table I. Field data collected on the phytoplankton of Takapoto Atoll between 1974 and 1998*.

Date of field trip	Measured parameters	References
August 1974, August 1975	B, P, C	Sournia and Ricard, 1975a,b; 1976
April–December 1977, March 1978	B	Guéredrat and Rougerie, 1978; Ricard et al., 1979
June 1990–September 1991	B	Buestel and Pouvreau, 2000
October 1993	B	Vacelet et al., 1996
June 1991–February 1994	B, P, S	Charpy et al., 1992; 1994; Charpy, 1996; Charpy and Blanchot, 1996; 1998
April 1996, April 1997	B, P, S, C	Sakka, 1999; Sakka et al., 1999, 2000
April 1996, April 1997	B, C	Loret, 1999; Loret et al., 2000
March 1997, August 1998	B, P, S	Pagès, 1998

* The type of data collected is coded as follows: B, biomass; P, primary production; S, size fractionation; C, taxonomic composition.

Table II. Phytoplankton biomass, production (incubation time in brackets) and assimilation numbers measured in Takapoto lagoon between 1974 and 1998.

Date	Biomass (chl *a*; µg·L^{-1})	Primary production (mg C·m^{-2}·day^{-1})	P/B (mg C·mg chl *a*$^{-1}$·h^{-1})	References
1974	0.10	275 (6 h)	–	Sournia and Ricard, 1975a
1975	0.46 ± 0.02	395 (6 h)	2.6	Sournia and Ricard, 1976
1977–1978	0.26 ± 0.16	–	–	Guéredrat and Rougerie, 1978; Ricard et al., 1979
1990–1991	0.28 ± 0.03	–	–	Buestel and Pouvreau, 2000
June 1991	0.31 ± 0.01	820 (4 h)	13–21	Charpy et al., 1992
1991–1994	0.27 ± 0.01	912 (4 h)	13.0	Charpy, 1996
1993	0.05 ± 0.11	–	–	Vacelet et al., 1996
1996	0.25 ± 0.04	777 (24 h)	12.0	Sakka, 1999
1997	0.23 ± 0.07	650 (24 h)	8.8	Sakka, 1999
1996	0.24 ± 0.06	–	–	Loret, 1999
1997	0.27 ± 0.08	–	–	Loret, 1999
1997	0.32	540 (8 h)	10.0	Pagès, 1998
1998	0.35	490 (8 h)	8.5	Pagès, 1998
1998		343 (46 h)		Pagès, 1998

was measured on several transects (*figure 1*), whereas the primary production was estimated only in the southern part of the lagoon. Between June 1990 and September 1991, a monthly survey of the phytoplankton biomass was conducted on 10 stations scattered over the lagoon (*figure 1*), and at two depths (8 m below the surface, 3 m over the bottom) (Buestel and Pouvreaud, 2000). This set of 10 stations was used in most of the following studies (e.g. Charpy et al., 1992, 1994; Charpy and Blanchot, 1996, 1998; Pagès 1998). In 1996–1997, the two companion studies (Sakka, 1999; Loret, 1999) used mainly station 9.

2.2. Methods

The phytoplankton biomass estimated by the chlorophyll *a* (chl *a*) concentration was the only parameter measured in all studies. The methods used for all parameters are shortly summarised below as they were already fully described in the referenced publications.

The chlorophyll *a* concentration was determined by the fluorimetric method according to Yentsch and Menzel (1963). Water samples were filtered either on Whatman GF/C filters (Sournia and Ricard, 1976; Vacelet et al., 1996; Buestel and Pouvreau, 2000), or GF/F filters (Charpy, 1996; Loret, 1999; Sakka, 1999). Size fractionated samples were obtained using Nuclepore 1 µm and 3 µm filters (Charpy and Blanchot, 1996; Sakka, 1999). Either acetone or methanol was used for extraction.

The ^{14}C method (in situ incubations) was used for the determination of primary production. The radioactivity added to the water samples was low (between 2 and 4 µCi) except in 1996–1997 (19 µCi) (Sakka, 1999). The incubation time was variable, from 4 h (Charpy, 1996) to 24 h (Sakka, 1999). As agreed now, short incubation times, below 12 h, provide estimates of the gross primary production, whereas the results of longer ones, are considered as estimates of the net primary production.

The taxonomic composition of the phytoplankton was only determined in 1974 (Sournia and Ricard, 1976) and in 1996–1997 (Loret, 1999; Sakka 1999). In these studies, the classical Utermöhl method (Utermöhl, 1958) was used and the cell counts were achieved on an inverted microscope. In addition, HPLC pigment analysis was undertaken in the study of the pearl oyster diet (Loret, 1999; Loret et al., 2000). However, this method only allowed the identification of the main phytoplankton classes.

3. RESULTS AND DISCUSSION

3.1. The phytoplankton biomass

The mean values of the phytoplankton biomass, as expressed by the chlorophyll *a* concentration, are presented in *table II*. The phytoplankton biomass ranged between 0.05 and 0.46 µg chl *a*·L^{-1}. The lowest values (0.05 µg chl *a*·L^{-1}) are reported by Vacelet et al. (1996). The highest ones reached 0.8 µg chl *a*·L^{-1} in several studies (Sournia and Ricard, 1976; Ricard et al., 1979; Pagès, 1998; Buestel and Pouvreau, 2000), and constituted a rather high value considering the oligotrophic environment. Most of the values reported ranged between 0.2 and 0.3 µg chl *a*·L^{-1}, i.e. a very narrow range considering the number of data involved (several hundreds) and the 24-years span of their measurement. Standard errors, when available, were low, mostly below 0.1 µg chl *a*·L^{-1} (*table II*). It can be concluded that, on the whole, the mean phytoplankton biomass did not significantly change between 1974 and 1998.

3.1.1. Spatial variations

The horizontal repartition of the phytoplanktonic biomass is somewhat debatable according to the differing results reported. On the one hand, Sournia and Ricard (1976) described higher biomass in the south

ern part of the lagoon in August 1974 (*figure 2a*). Ricard et al. (1979) confirmed this spatial heterogeneity in most of their surveys in 1977–1978. Similar observations were made by Sakka (1999) (*figure 2c*), and Pagès (1998) (*figure 2d, 2e*). On the other hand, Buestel and Pouvreau (2000), using Anova analysis on their monthly data, concluded to a homogeneous repartition of the phytoplanktonic biomass in 1990–1991 (*figure 2b*). These apparently opposite conclusions may result from the different temporal scale considered. The heterogeneity of the lagoon was observed during short field trips, most of them taking place during the austral winter. On the contrary, the 1990–1991 data were collected monthly during one year and embraced various meteorological conditions, especially regarding the wind speed. From these opposite results, it seems that the phytoplankton biomass is evenly distributed at the year scale but that some heterogeneity may temporarily occur. This situation can be explained by several factors: 1) the absence of reef-flat spillways in the south, implying a longer residence time of waters in that part of the lagoon, 2) the prevailing winds blowing from the northeast and accumulating the water in the southern part of the atoll, and 3) the location of the village in the most confined part of the lagoon and the possible enrichment of waters due to anthropogenic effluents. The existence of this heterogeneity seems to be related to rather calm weather, which allows a certain stratification to take place (Charpy, 1996). A moderate easterly wind results in an accumulation in the south but stronger winds induce a faster recirculation that leads to homogenize the water masses in the lagoon. It must however be noted that higher phytoplankton biomasses were often observed in the south part of the lagoon where the pearl oysters rearings are the densest. A small bloom of chlorophytes was observed in December 1996 in this part of the atoll. Fortunately, it did not involve a strong mortality of the oysters, but this threat must not be ignored.

An increase of the phytoplankton biomass with depth was observed in 1974–1975 (Sournia and Ricard, 1975a; 1976), especially in the deeper part of the lagoon. A significant difference ($P < 0.05$) of the chl *a* concentration between the two sampled depths is also reported in 1990–1991 (Buestel and Pouvreau, 2000). However the difference is slight (0.25 ± 0.2 vs 0.28 ± 0.02 µg chl $a \cdot L^{-1}$). On the contrary, Charpy (1996) observed that the chlorophyll *a* was evenly distributed in the water column except during calm conditions where biomass maximum were encountered between 15 m and 25 m depth. Similarly, no significant variation with depth was observed in 1996 and 1997 (Sakka, 1999).

3.1.2. Temporal variations

Significant nycthemeral variations of the chlorophyll a concentrations were observed by Charpy et al. (1994) and Sakka (1999). This increase is mainly

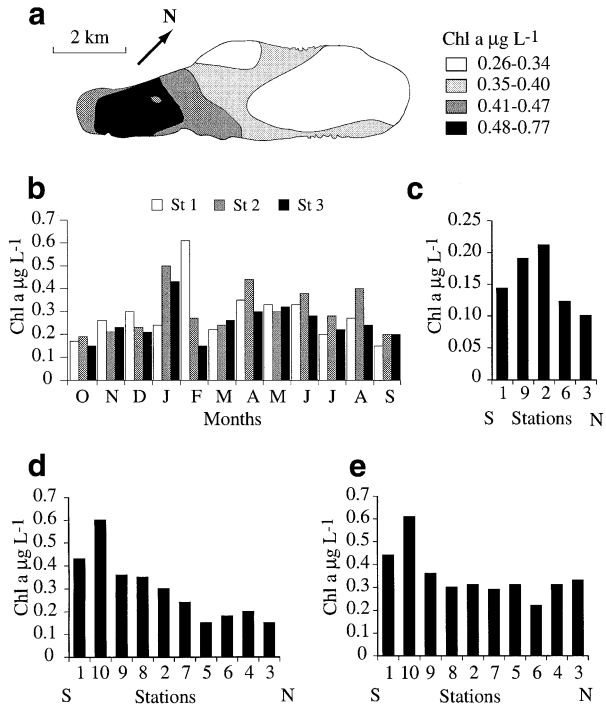

Figure 2. Distribution of the chlorophyll *a* concentration: **a.** in 1974 (Sournia and Ricard, 1976); **b.** in 1990–1991 (Buestel and Pouvreau, 2000); **c.** in 1996 (Sakka, 1999); **d.** in March 1997 and **e.** in August 1998 (Pagès, 1998). The stations are ordered according to their related south- to-north position.

achieved by the < 1 µm and the > 3 µm fractions (Sakka, 1999), and is negatively correlated to the abundance of the < 35 µm protozoa (Sakka, 1999). At the seasonal scale, an increase in the phytoplankton biomass was sometimes identified during the austral summer (Ricard et al., 1979; Buestel and Pouvreau, 2000). But Charpy (1996) did not detect any seasonal effect in 1991–1994.

The pluriannual scale deserves attention, as chlorophyll data spread over 24 years are unusual in coral reef environments. From the data available (*table II*), no significant long-term change in the phytoplankton biomass can be detected. However, the pearl oysters mariculture greatly increased since 24 years. The first pearl farm was established in 1971. They were more than 40 in 1985 (Coeroli, 1986), and are still 33 now. It is broadly estimated that 1 million pearl oysters is now cultivated. These bivalves, mainly feeding on phytoplankton, could have reduced the phytoplanktonic biomass. The absence of long-term variations in the phytoplankton biomass is an indirect confirmation of a negligible influence of pearl oysters on phytoplankton as reported by Niquil (1998) and Niquil et al. (2001).

3.2. Primary production and assimilation numbers

The primary production measured between 1974 and 1998 varied between 275 and 912 mg C·m^{-2}·day^{-1} i.e. in a four-fold range (*table II*). The lowest values were measured in 1974 (275 mg C·m^{-2}·day^{-1}) (Sournia and Ricard, 1975a), and 1975 (395 mg C·m^{-2}·day^{-1}) (Sournia and Ricard, 1976). However, as reported by Charpy (1996), these values are probably underestimated due to problems in the incubation techniques (e.g. cleanliness of the incubation bottles, use of glass instead of polycarbonate). Most of the values reported since 1990 exceeded 500 mg C·m^{-2}·day^{-1} and reached 912 mg C·m^{-2}·day^{-1} (Charpy et al., 1994). These values are estimations of the gross primary production, as the incubation times ranged between 4 h and 8 h. On the contrary, the values measured in 1996–1997 (Sakka, 1999) were obtained after incubation times of 24 h and were therefore net primary productions. Pagès (1998) used increasing incubation times in order to evaluate the net/gross production ratio and reported a net/gross production ratio of 0.66. If this ratio is applied to the 1996–1997 results, the resulting gross primary production is ca. 1000 mg C·m^{-2}·day^{-1}, i.e. a value similar to the one measured during the first phase of PGRN.

Few data are available to evaluate the spatial or temporal variations of the primary production. Charpy (1996) reported the absence of a seasonal variation as already underlined in similar environment (Furnas and Mitchell, 1987). Similarly, no spatial differences can be outlined from his measurements in 1991–1994 (Charpy et al., 1994). Considering the vertical repartition of the primary production, Charpy (1996) observed that maximum photosynthesis occurred at 10 m depth. Sakka (1999) made the same observations but concluded to no significant vertical variations.

The assimilation numbers, i.e. the ratio of the production to the biomass, showed values mostly exceeding 8 and reaching 13 mg C·mg chl a^{-1} h^{-1} (*table II*). These high values indicate that the phytoplankton is actively growing. This characteristic of the phytoplankton production in coral reefs environments has already been underlined by several authors (e.g. Ricard and Delesalle, 1981; Legendre et al., 1988).

3.3. Phytoplankton composition

The composition of the phytoplankton can firstly be described by the different size fractions. As it was evidenced in most water masses, phytoplankton biomass (in terms of chl *a*) is principally represented by the < 1 µm fraction (Charpy, 1996; Sakka, 1999), which contributed for more than 60% in Takapoto lagoon (*figure 3*). Similarly, the picophytoplankton achieved more than 50% of the primary production (*figure 3*). On the contrary, the assimilation number P/B is higher in the > 3 µm fraction. Charpy (1996) estimated the P/B in the > 3 µm fraction to be

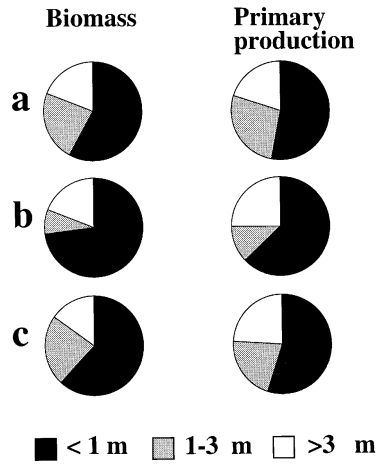

Figure 3. Size-fractionation of the phytoplankton biomass and primary production: **a.** in 1991–1994 (Charpy 1996); **b.** in 1996; **c.** in 1997 (Sakka, 1999).

16.9 ± 1.1 vs 10.5 ± 0.6 mg C·mg Chl a^{-1}·h^{-1} in the < 1 µm fraction. Similarly, Sakka (1999) observed higher P/B in the 1–3 and > 3 µm fractions: respectively 130–220 and 130–200 mg C·mg chl a^{-1}·day^{-1}.

Very few data are available on the phytoplankton of size higher than 3 µm. The microsocopic examination showed the absence of cells > 50 µm (*figure 4*) (Loret, 1999). In addition, samples obtained in 1996 with a net of 70 µm mesh size did not contain any phytoplanktonic cell.

The taxonomic composition of phytoplankton is still poorly known. The picophytoplankton was mainly

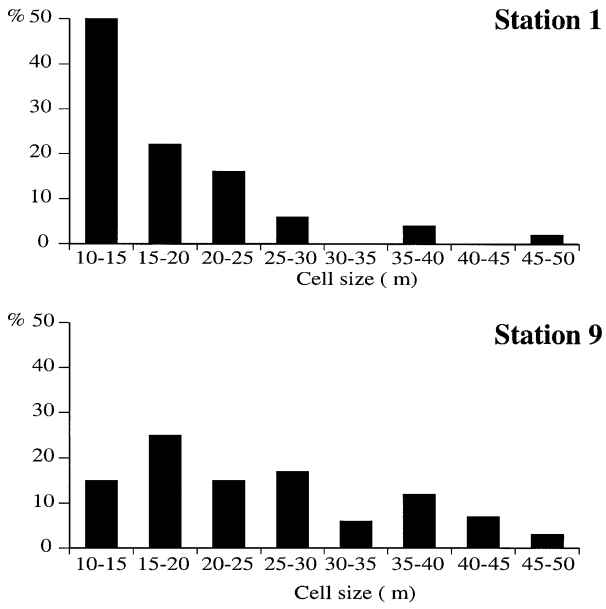

Figure 4. Size distribution of the phytoplankton > 10 µm at two stations in 1997 (Loret, 1999).

composed of *Synechococcus* whereas *Prochlorococcus* constituted only 5% of this size class (Charpy et al., 1992; Charpy and Blanchot, 1996, 1998). Concerning the nano- and the microphytoplankton, three major groups (diatoms, dinoflagellates and coccolithophorids) predominated in 1974 (*table III*) (Sournia and Ricard, 1976). The diatoms were the most diversified group whereas the dinoflagellates were the most abundant. In 1996–1997, mostly pico- and nanophytoplankton were observed, the latter being small phytoflagellates (*table III*) (Loret, 1999; Sakka, 1999; Loret et al., 2000; Sakka et al., 2000). The HPLC pigment analysis outlined the predominance, in term of chlorophyll *a*, of picocyanobacteria and prymnesiophytes whereas chlorophytes, diatoms and cryptophytes were the secondary groups (Loret et al., 2000). The chlorophytes predominated in the > 3 µm fraction in the southern part of the atoll (station 1). Chlorophytes were still present at stations 9 and L (*figure 1*) but in lower proportions compared with prymnesiophytes. Cell numbers gave similar results with a predominance of dinoflagellates (> 10%) and of chlorophytes which accounted for > 50% of the enumerated cells (Sakka, 1999). The dinoflagellates were mostly heterotrophic as their specific pigment, the peridinin, was not detected by the HPLC method (Loret, 1999).

The taxonomic composition of phytoplankton seems to have drastically changed between 1974 and 1996. The taxonomic list given by Sournia and Ricard (1976) included some of the biggest phytoplankton cells known, e.g. *Ethmodiscus appendiculatus*, a diatom whose size can reach 1500 µm (Ricard, 1970). Similarly, one of the most abundant dinoflagellate was *Ceratium furca* (10^5 to 10^6 cells·L^{-1}) whose size reaches 100 µm. None of these large species were observed in 1996–1997 while *C. furca* is one of the commonest dinoflagellate in the phytoplankton of atolls (Delesalle, unpublished data). A large diatom, *Proboscia alata*, grew in significant numbers (10^5 cells·L^{-1}) in enriched bioassays (Sakka et al., 1999). Obviously, investigation methods changed between 1974 and 1996. However, the absence of phytoplankton cells in the net samples performed in 1996 and 1997 evidences a shift of the phytoplankton community towards the smaller sizes. Due to the absence of observation between 1974 and 1996, it cannot be stated whether this shift is permanent, or just reveals a temporary situation at the time of the sampling. In fact, the taxonomic composition of phytoplankton received little attention in the 1991–1994 studies and its spatial and temporal variations remain quite unknown. These variations could be rapid: the chlorophytes were predominant in April 1996 and 1997. They caused a small bloom in the southern part of the lagoon in December 1996, but they cannot be found again in November 1998.

The reason of this shift towards smaller sizes of phytoplankton is not yet clearly understood. It could be enticing to relate it to the development of pearl oyster farming. The pearl oysters do not seem to modify the phytoplankton biomass (Niquil, 1998), but most of this biomass is made of picoplankton. Pearl oysters are known to efficiently retain particles between 2 µm and ca. 100 µm (Jonquières et al., 1994) but little is known on the upper limit of this range. This shift could result from a modification of the structure of the planktonic network, especially concerning the large zooplankton, which is the natural predator of the microphytoplankton. However, the available data on the mesozoopolankton are too scanty to substantiate this hypothesis. More detailed investigations of this compartment are needed to clarify the particular situation of the phytoplankton in Takapoto Atoll.

4. CONCLUSION

From the results obtained since 1974, the mean values of the phytoplankton biomass and primary production can be estimated. A biomass of 0.2–0.3 µg chl *a*·L^{-1} and a net primary production of 0.6–0.8 mg C·m^{-2}·day^{-1} can be considered as mean values to be used in models. On the whole, no significant temporal or spatial variations can be outlined, neither long-term variations that could result from the development of the pearl-oyster mariculture. However, a temporary heterogeneity may occur and lead to small algal blooms, mostly located in the south part of the atoll. The size structure of the phytoplankton showed the well-known dominance of the picoplankton, mainly represented by *Synechococcus*. In contrast to the biomass and the primary production, the taxonomic composition of the phytoplankton of Takapoto Atoll received little and undoubtedly insufficient attention as no studies were done between 1974 and 1996. The interpretation of several results is hampered by the resulting lack of knowledge, e.g. the observed shift of the phytoplankton composition towards smaller size, the implications of the selection in the pearl oyster diet, or the risk of algal blooms. Recent researches, focused on potentially blooming or toxic species (Delesalle and Chrétiennot-Dinet unpublished data), identified several prymnesiophytes, especially *Chrysochromulina* and *Phaeocystis* species. The presence of these species would deserve a permanent monitoring program of the taxonomic composition of phytoplankton, still to be set up.

Acknowledgements. Research was carried out as part of the '*Programme général de recherche sur la nacre*' (PGRN2, General Research Program on Pearl-Oyster, second phase), with financial support of the Ministry for Education, Research and Technology, the Ministry for Overseas, and the Government of French Polynesia. We express our gratitude to the director of the '*Service des ressources marines*' in Takapoto Atoll, G. Haumani, and his team for efficient assistance in the field. We also thank the reviewers for their useful comments.

Table III. List of phytoplankton species identified in 1974 and in 1996–1997 in Takapoto Atoll.

1974*

Coccolithophorids
Undetermined coccolithophorids

Cyanophytes
Lyngbya sp.
Nostoc sp.
Oscillatoria sp.
Spirulina sp.

Diatomophyceae
Achnanthes brevipes
Actinoptychus undulatus
Amphiprora alata
Amphora arcus
Amphora dubia
Amphora graeffii
Amphora janischii
Amphora spectabilis
Amphora staurophora
Amphora turgida
Amphora sp.
Asterolampra marylandica
Auricula complexa
Campylodiscus brightwellii
Chaetoceros curvisetum
Chaetoceros sp.
Chrysanthemodiscus floriatus
Climacosphenia moniligera
Cocconeis sp.
Coscinodiscus nodulifer
Coscinodiscus sp.
Cylindrotheca closterium
Diploneis bombus
Diploneis crabro
Diploneis debyi
Diploneis subcincta
Ethmodiscus appendiculatus
Ethmodiscus gazellae
Gyrosigma balticum
Leptocylindrus sp.
Licmophora ehrenbergii
Licmophora sp.
Mastogloia decipiens
Mastogloia erythraea
Mastogloia sp.
Melosira sulcata
Navicula longa
Navicula lyra
Navicula
Nitzschia distans
Nitzschia maxima
Nitzschia panduriformis
Nitzschia spathulata
Nitzschia valida
Nitzschia sp.
Planktoniella sol
Pleurosigma rigidum
Pleurosigma sp.
Rhabdonema adriaticum
Rhizosolenia alata
Rhizosolenia calcar-avis
Rhizosolenia hebetata
Rhizosolenia styliformis
Striatella unipunctata
Synedra laevigata
Synedra ulna
Synedra undulata
Synedrosphenia gomphonema
Trachynieis aspera
Triceratium formosum
Triceratium shadboltianum
Tropidoneis lepidoptera
Dinophyceae
Amphidinium schroederi
Amphidinium sp.
Amphisolenia bidentata
Centrodinium sp.
Ceratium furca
Ceratium fusus
Ceratium macroceros
Ceratocorys armata
Ceratocorys horrida
Dinophysis doryphorum
Dinophysis hastata
Dinophysis sp.
Exuviaella sp.
Glenodinium sp.
Goniodoma polyedricum
Goniodoma sp.
Gonyaulax digitale
Gonyaulax kofoidii
Gonyaulax monacantha
Gonyaulax polygramma
Gonyaulax spinifera
Gonyaulax sp.
Gymnodinium spp.
Gyrodinium spp.
Ornithocercus magnificus
Ornithocercus quadratus
Oxytoxum sp.
Peridinium depressum
Peridinium cf. globulus
Peridinium grande
Peridinium ovum
Peridinium pyriforme
Peridinium sp.
Prorocentrum micans
Pyrophacus horologium

1996–1997**

Chlorophytes
Chlamydomonas sp.

Prasinophytes
Nephroselmis sp.
Pyramimonas

Prymnesiophytes
Coccolithophorids
Acanthoica sp.
Cricosphaera sp.
Corisphaera sp.
Emiliania huxleyii
Gephyrocapsa oceanica
Syracosphaera

Chrysochromulins
Chysochromulina sp.

Cryptophytes
Cryptomonas sp.
Leucocryptos sp.
Plagioselmis sp.
Rhodomonas sp.

Cyanophytes
Microscystis sp.
Oscillatoria sp.

Diploneis sp.
Fragillaria sp.
Licmophora sp.
Mastogloia sp.
Navicula sp.
Nitzschia closterium
Nitzschia ventricosa
Nitzschia sp.
Tropidoneis sp.

Dinophyceae
Alexandrium sp.
Amphidinium sp.
Blepharocystis sp.
Diplopsalis sp.
Dinophysis sp.
Gonyaulax polyedra
Katodinium sp
Oxytoxum sp. *1*
Oxytoxum sp. *2*
Pronoctiluca sp.
Prorocentrum mexicanum
Prorocentrum scalpellum
Prorocentrum triestinum
Protoperidinium sp.
Scripsiella sp.

* Sournia and Ricard, 1976; ** Loret, 1999; Sakka, 1999

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