Aquat. Living Resour. 14 (2001) 183−193

S0990744001011135/FLA

Hydrology and trophic state in Takapoto Atoll lagoon: comparison with other Tuamotu lagoons

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Received 20 June 2000; accepted 13 February 2001

Abstract − Several studies have found that, since 1975 at least, the atoll lagoon of Takapoto exhibits high salinities and high planktonic chlorophyll concentrations. We used observations gathered in Takapoto and 23 other atoll lagoons between 1995 and 2000 to study the water renewal rate (determined by different approaches) of Takapoto relative to that of the other lagoons. This rate is controlled by reef rim aperture, which is abnormally low in Takapoto. Across this set of lagoons, average water residence time was correlated with salinity, and with two descriptors of water column biological properties, chlorophyll and dissolved organic matter contents. In parallel to these bulk quantitative variations, qualitative variations were found inside this trophy gradient, concerning the size of primary producers (proportion of cells > 2.7 μm) and the composition of seston (relative phosphorus content). Takapoto Lagoon fits into a gradient of water residence time that controls the overall trophic web organization. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

chlorophyll / dissolved organic matter / trophic state / water renewal rate

Résumé − Hydrologie et état trophique du lagon de l'atoll Takapoto : comparaisons avec les autres lagons de Tuamotu. Le lagon de Takapoto, sujet de plusieurs études depuis 1975, présente une salinité élevée et une forte biomasse phytoplanctonique. Nos observations sur Takapoto et sur 23 autres lagons entre 1995 et 2000 permettent de situer Takapoto dans un gradient de renouvellement de l'eau du lagon du fait des entrées d'eau océanique. Ce flux, que nous déterminons de différentes façons, est contrôlé par les ouvertures du récif qui sont anormalement réduites (par rapport aux autres lagons) à Takapoto. Sur cet ensemble de lagons, le temps moyen de résidence des eaux est corrélé à la salinité et à deux descripteurs biologiques : la concentration en chlorophylle et la teneur en matière organique dissoute. Parallèlement à ce gradient trophique quantitatif, nous constatons des variations qualitatives, dans la taille des producteurs primaires (proportion d'organismes > 2,7 μm) et dans la composition du seston (teneur relative en phosphore). Le lagon de Takapoto s'insère bien dans un gradient de temps de résidence qui se répercute sur l'organisation générale du réseau trophique planctonique. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

chlorophylle / matière organique dissoute / état trophique / taux de renouvellement de l'eau

1. INTRODUCTION

The atoll of Takapoto was selected as a study site for the Man and Biosphere (MAB) program in the 1970s. Initial studies showed that the lagoon was landlocked (Sournia and Ricard, 1975, 1976) or semi-closed (Magnier and Wauthy, 1976; Guérédrat and Rougerie, 1978). Its high salinity (38–40 p.s.u.) could be ex

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plained by low water exchanges with the surrounding ocean. High phytoplankton biomasses were also found despite very low nutrient concentrations. The "paradox of the atolls" (high production in extremely oligotrophic waters) has been explained for benthic organisms by considering small scale hydrodynamical processes (Baird and Atkinson, 1997; Thomas and Atkinson, 1997) in which high water renewal rate compensates for the low nutrient concentrations. At the lagoon scale, however, a compilation of different studies on several lagoons, including Takapoto, found that phytoplankton biomass increases with residence time (Delesalle and Sournia, 1992).

We collaborated in a comparative study carried out in 1995–1997 on 12 atolls during the TypAtoll program (Dufour and Harmelin-Vivien, 1997). This typological approach showed that atoll morphology, especially reef rim characteristics (Andréfouët et al., 2000), influenced water column properties (Dufour et al., 1999; Charpy et al., 1997) and macrobenthic organisms (Adjeroud et al., 2000). A further program, PGRN (*Programme général de recherche sur la nacre*), was focused on the effects of environment (in the broadest sense) on pearl oyster culture. These programs enabled us to gather a homogeneous set of measurements, concentrating on a few variables, in a total of 24 atoll lagoons including Takapoto.

We have found a gradient of water residence time that controls the trophic state of the lagoonal planktonic web. Well-flushed lagoons are more oligotrophic, with low concentrations of bulk estimators such as chlorophyll or dissolved organic matter. However, the qualitative food web organization also changes with increasing oligotrophy, as shown by proxy descriptors of seston composition, such as size ratio (2.5 μm vs. 0.7 μm for chlorophyll) or chemical composition (particulate organic phosphorus vs. chlorophyll). These qualitative differences could explain for instance the rather poor growth of pearl oysters in the mesotrophic lagoon of Takapoto, which fits well into the above trends.

The comparative approach reported in this paper finds that Takapoto, while clearly not a typical Polynesian atoll lagoon, is only a somewhat extreme case in a continuum in which atoll lagoon properties are controlled by hydraulics. It will be shown that properties of lagoons around high islands follow a similar general trend.

2. MATERIAL AND METHODS

2.1. General setting

The atoll of Takapoto (145°12'W, 14°37'S) is one of the northermost of the Tuamotu Archipelago and experiences a humid tropical climate. Annual rainfall is about 1500 mm, with a warm (28°C) humid season between October and April. Evaporation of free water (70% of Penman values) is equivalent to rainfall on an annual basis, but with seasonal variations. The prevailing winds are the easterly Trades, blowing strongest during the cool (25°C) period from May to September. Oceanic salinities are around 36 p.s.u. (Rancher and Rougerie, 1995).

The tidal amplitude around Tahiti and the western Tuamotu is about 0.3 m for spring tides, and about 0.1 m or less for neap tides. The water temperature in the lagoons closely follows the air temperature.

Takapoto fits the generally accepted paradigm of an atoll, with a central lagoon surrounded by a chain of islets separated from each other by shallow (0.3–0.8 m) reef-flat spillways (the *hoa*; Guilcher, 1988). A pass, i.e. a deep (> 10 m) tidal connexion to the ocean, may exist on some atolls, but not on Takapoto.

The TypAtoll lagoons were visited 3 times (November 1994, November 1995, and March 1996). Seven 'core' PGRN atolls (*table I*) were each visited twice between 1997 and 1999, without definite timing. The other five PGRN atolls were visited only once between 1999 and 2000. The last stages of a bloom were observed in Hikueru lagoon in March 1994. Occasional field trips were made to two high islands (Raiatea and Mangareva) with a central mountain surrounded by a lagoon limited by a barrier reef.

2.2. Physical measurements

On each of our 4 surveys of Takapoto (*table II*), we visited ten stations (*figure 1*) defined during earlier

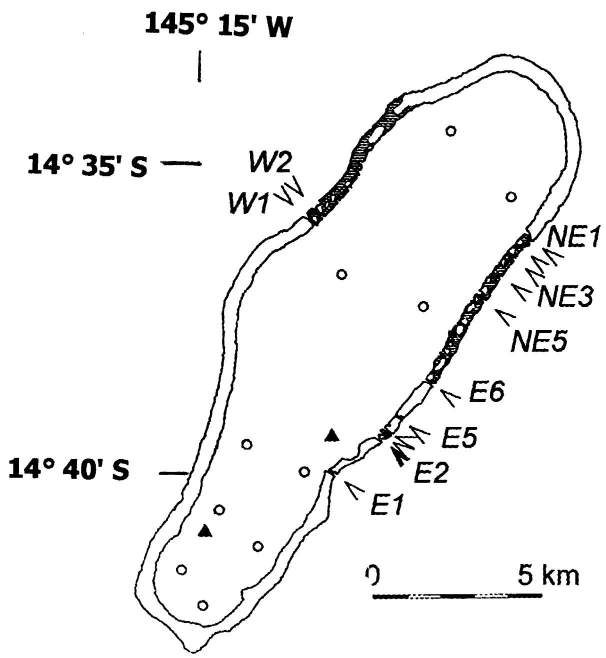

Figure 1. General map of Takapoto Atoll. The locations of active *hoa* (reef-flat spillways) are marked by outside arrows. Hatched areas are indicated as submerged on marine charts. The 10 routine stations (○) and the salinity monitoring sites (▲) are indicated.

Table I. General characteristics of lagoons studied.

Lagoon	Pass	Area (km^2)	T_{RAV} (days)	A_{254} (m^{-1})	B_{tot} (µg·L^{-1})	Σ (p.s.u.)
Ahe*	+	145	34	0.72	0.21	–
Amanu	+	210	39	0.51	0.28	36.34
Apataki*	+	683	101	0.70	0.20	–
Arutua**	+	516	60	0.73	0.20	36.36
Fakarava**	+	1112	75	0.66	0.24	36.34
Hao*	+	497	90	0.62	0.18	36.11
Haraiki	–	10	3	0.83	0.41	35.94
Hikueru	–	82	37	0.76	0.28	36.59
Hiti	–	15	3	0.77	0.40	36.69
Kauehi	+	315	77	0.50	0.33	36.44
Makemo*	+	603	15	0.72	0.22	–
Mangareva*	H	–	–	0.69	0.21	–
Manih**i	+	165	130	0.91	0.42	36.49
Marokau	–	217	55	0.63	0.26	37.08
Mataiva*	+	25	21	1.34	1.04	36.69
Nihiru	–	79	17	0.70	0.40	36.62
Raiatea*	H	–	–	0.51	0.21	–
Rangiroa**	+	1592	155	0.62	0.35	–
Reka-Reka	–	0.7	81	1.41	0.91	37.28
Taiaro	–	12	1761	2.34	1.17	42.88
Takapoto**	–	81	268	1.02	0.41	38.60
Takaroa**	+	89	76	0.78	0.24	–
Tekokota	+	5	0.3	0.42	0.07	36.57
Tepoto S.	–	2	0.6	0.66	0.43	36.28
Tikehau**	+	394	60	0.53	0.28	–
Tuanake	–	26	17	0.57	0.28	36.25
Vairao**	H	–	–	0.70	0.57	–
Ocean				0.37	0.09	36.20
Hikueru bloom*	–	82	171	1.24	1.24	–
Takaroa bloom*	+	89	448	0.87	0.65	–

Lagoon area and residence time are not defined for high island lagoons or for ocean. T_{RAV}: average water residence time; A_{254}: UV light absorption at 254 nm; B_{tot}: chlorophyll concentration; Σ: salinity; * PGRN program lagoons; ** 'core' PGRN lagoons; H: lagoon around a high island, behind a barrier reef.

Table II. Surveys in Takapoto atoll lagoon: date and general conditions.

Date	Swell height (H_{SAT}, m)	Wind speed (m·s^{-1})	In-flow (ΣD, m^3·s^{-1})
19 March 1997	1.5	1.5	2
13 August 1998	2.3	5.5	26
9 July 1999	1.8	6.9	37
23 August 2000	1.7	6.9	56

studies (Rougerie, 1979; Sakka et al., 1999). A monitoring program started by SRM (*Service des ressources marines*) in August 2000 (in relation with oyster growth) involved 2 sites.

On the atoll, wetted width, water depth and current speed were determined in each *hoa*, the current speed by timing drifters on a 10 m-long floating line. The sum ΣD of measured flow rates gave an estimate of incoming oceanic water under low to medium wave energy conditions. The width of each *hoa* has also been determined from SPOT satellite imagery (image taken on 13 July 1991, for Takapoto; Andréfouët et al., 2000). We defined a minimum width L'_{min} corresponding to very calm seas, and a maximum width L'_{Max} corresponding to periods of high waves with wave height H_{SAT} of approximately 4–5 m.

Wave height, H_{SAT}, was determined from satellite data (TOPEX/Poseidon and ERS), averaged in a square of 143–153°W and 9–20°S between March 1997 and September 2000. Water level in Takapoto Lagoon was monitored (each week, starting in May 1997) by manually reading a scale located at the southern end of the lagoon.

2.3. Water properties

Salinities were determined on samples with an induction salinometer. Dissolved organic matter (DOM) content was estimated from light absorption at 254 nm, A_{254} (Pagès et al., 1997). Chlorophyll was assessed using Whatman GF/F or GF/D filters. Methanol extracts were processed by fluorimetry (Turner 111 or 112), with spectrophotometric calibration according to Porra's (1991) equations. We deal with total chlorophyll, not that corrected for phaeopigments. Particu late organic phosphorus (*POP*) was measured using calcinated GF/F filters after persulphate oxidation (Aminot and Chaussepied, 1983; Charpy et al., 1997).

3. RESULTS

3.1. Wave climate

In the period sampled (728 days), average wave height H_{SAT} was 2.0 ± 0.5 m, with a median of 2.1 m. Waves of $H_{SAT} \geq 3$ m were found 3.8% of the time, and of $H_{SAT} \geq 3.5$ m, 1% of the time. This indicates that field observations would often be made under a rather calm wave climate. Local wind speed is a poor predictor of wave height ($r^2 = 0.04$ for $n = 159$ between May 1997 and July 1998).

Most wave energy comes from the south, with heavier seas from the southwest (consistently about 0.8 m higher seas west of 150°W). For the set of 24 atolls studied, the relative aperture orientation agrees well with ocean wave energy distribution among 8 sectors (N, NE, E, etc.)

3.2. Aperture toward the ocean

The lagoon of Takapoto has an area of 81 km², and a mean depth of 23 m (Sournia and Ricard, 1975; Guérédrat and Rougerie, 1978). Among the set of 24 atolls studied, most overall descriptors are mutually correlated. For instance, mean depth is correlated with lagoon area, and Takapoto follows the general trend.

Marine maps of Takapoto indicate numerous, mile-wide gaps between islets. These gaps correspond in fact to bare above-water expanses, and there are few active *hoa*, most of them less than 20 m wide (*table III*). Satellite imagery gives a total aperture of $L'_{min} = 0.1$ km under calm wave conditions, and $L'_{Max} = 1.7$ km under heavy seas. These numbers may be considered as constant during the period covered by published studies. For the set of the 23 other atolls, apertures (L'_{min} and L'_{Max}, in kilometres) are related to lagoon area, A, expressed in square kilometres as follows (*figure 2*): $L'_{min} = 2.16 \times \exp(0.0039 \times A)$, $r^2 = 0.68$, and $L'_{Max} = 6.32 \times \exp(0.0031 \times A)$, $r^2 = 0.69$.

Table III. Characteristics of the *hoa* on Takapoto: eastern, northeastern and western sectors.

Hoa	Wetted width (m)	Water depth (m)	Current speed ($m \cdot s^{-1}$)	In-flow ($m^3 \cdot s^{-1}$)	Date	Reference
E1	20	0.6	0.5	6.0*	1975–1978	1
	35	0.15	0.06	0.3	17 March 1997	3
	35	0.5	0.5	7.1	15 August 1998	3
	35	0.4	0.65	8.5	16 August 1998	3
	38	0.3	0.46	4.8	10 July 1999	3
	42	0.35	0.5	7.3	25 August 2000	3
E2	80	0.7	1.5	84.0*	1975–1978	1
	80	0.2	0.3	4.8*	August 1975	2
	80	0.25	0.12	2.0	17 March 1997	3
	85	0.5	0.4	18.3	15 August 1998	3
	100	0.3	0.95	28.8	10 July 1999	3
	100	0.35	1.1	36.3	25 August 2000	3
E3	30	1.0	0	0	17 March 1997	3
E4	35	0.6	0	0	17 March 1997	3
E5	20	0.5	0	0	17 March 1997	3
E6	40	0.6	0	0	17 March 1997	3
NE1	10	0.2	–0.5	–1.0	13 August 1998	3
	52	0.1	0.74	3.9	9 July 1999	3
	55	0.1	0.47	2.6	23 August 2000	3
NE2	30	0.2	0.66	4.0	23 August 2000	
NE3	60	0.15	0.64	5.8	23 August 2000	3
W1	20	0.6	1.0		1975–1978	1
	20	0.5	0.01	0.1	17 March 1997	3
	18	0.8	0.33	4.8	21 March 1997	3
	6	0.1	0.7	0.3	23 August 2000	3
W2	~3	0.2	0	0	17 March 1997	3
Total observed maximum average				110.7*	1975–1978	
				9.5	1975	2
				2.4	March 1997	3
				26.4	August 1998	3
				37.5	July 1999	3
				56.3	August 2000	3

* Recalculated from authors' data. References: (1) Guérédrat and Rougerie, 1978; (2) Ricard et al., 1978; (3) this study.

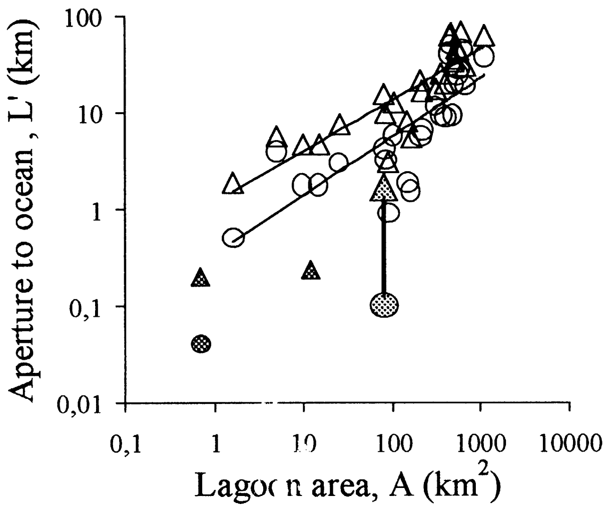

Figure 2. Relation between lagoon area A and reef rim aperture under maximum (▲) and minimum (○) swell conditions for a set of 25 atolls. Filled symbols correspond to closed (Taiaro) or semi-closed (Reka-Reka) atolls. Symbols for Takapoto are joined by vertical bar.

Note that, if these regressions ($P < 0.01$) represent the norm for Tuamotu atolls, Takapoto atoll should have an L'_{min} of approximately 3 km instead of 0.1 km.

We used the apertures determined from satellite data to compute potential flows, ΣQ, corresponding to minimum, average and maximum swell heights. We obtain for Takapoto $\Sigma Q_{min} = 8\ m^3{\cdot}s^{-1}$, $\Sigma Q_{AV} = 80\ m^3{\cdot}s^{-1}$, and $\Sigma Q_{Max} = 810\ m^3{\cdot}s^{-1}$. On other atolls, it was found that the computed flows agree with field measurements ($r^2 = 0.94$ for $n = 42$). We calculated average water residence time, T_{RAV}, as the ratio of lagoon volume to average water input rate; it is equivalent to Takeoka's (1984) turnover time. For Takapoto, the average residence time is 268 days, with extreme values of 2695 days (7.4 years) and 27 days. For the other 23 atoll lagoons, T_{RAV} ranges between a low of several days and a maximum (for Taiaro, a closed lagoon) of 1700 days (5 years; see *table I*). Aperture L' cannot be determined for a barrier reef, so that ΣQ and T_R are not available for lagoons around high islands.

3.3. Water exchanges

An outgoing flow was observed once on Takapoto (August 13, 1998), approximately two weeks after the lagoon had been filled up by high seas (see below).

Inflow rates in the various *hoa* on Takapoto ranged between nil and 30 $m^3{\cdot}s^{-1}$ (*table III*). The tidal effect was generally negligible, except in the least active *hoa* under low wave conditions. Specific flow rates, relative to wetted width, ranged between nil and an observed maximum (on 25 August 2000) of 0.5 $m^2{\cdot}s^{-1}$, with a current speed of 1.3 $m{\cdot}s^{-1}$. A specific flow rate is closely related to swell height. The sum of measured flows of oceanic water through the *hoa* into the lagoon ranged between a minimum of 2 $m^3{\cdot}s^{-1}$ and a maximum of 56 $m^3{\cdot}s^{-1}$ (*table II*), the latter under very moderate seas.

In Takapoto, the lagoon level shows relatively high amplitude variations (*figure 3*) lasting about 15 days. This time scale eliminates possible seiches, and lagoon level shows strictly no relationship with local wind ($r^2 = 0.04$ for $n = 159$, between May 1997 and July 1998). Lagoon level (ζ, in centimetres) and H_{SAT} yield no statistically significant trend with all available data ($n = 447$). During each separate episode of high seas, ζ rises and falls (*figure 4*) in causative relation with H_{SAT} ($r^2 = 0.72$–0.90 for $n = 6$–8; *table IV*). As an indirect confirmation of this relationship, the outgoing flow through the pass of Raroia Atoll was correlated with H_{SAT} ($r^2 = 0.55$ for $n = 39$).

Lagoon level variations give an estimation of incoming water flow. The surges shown in *figure 4* correspond to net inflows of 100–150 $m^3{\cdot}s^{-1}$ for H_{SAT} of 3–4 m. The outflow rates, during the emptying

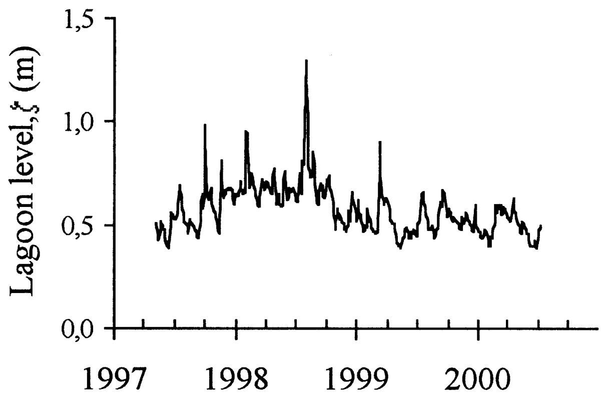

Figure 3. Variation of Takapoto Lagoon level, from 3 manual readings per week, between May 1997 and September 2000.

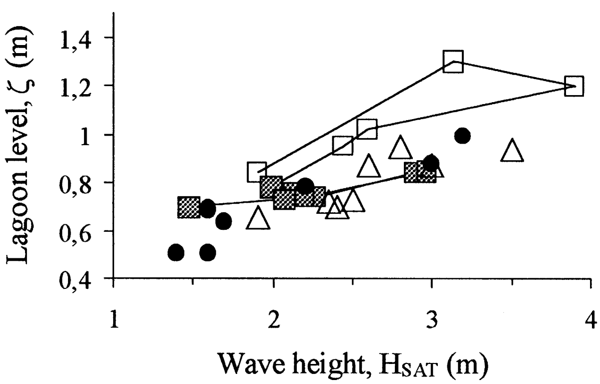

Figure 4. Response of lagoon level to sea state during separate episodes of high seas (△: 26 January–11 February 1998; □: 26 July–10 August 1998; ▩: 10 August–28 August 1998; ●: 4–20 September 2000).

Table IV. Examples of flow rates calculated from lagoon level variations, and regression between wave height H_{SAT} and lagoon level ζ.

	Flow rates ($m^3 \cdot s^{-1}$)			Regression	
Dates	net in	net out	gross in	r^2	*n*
26 July–10 August 1998	+107	–56	163	0.76	6
10–28 August 1998	+30	–21	51	0.82	7
26 January–11 February 1998	+98	–44	142	0.72	8
4–20 September 2000	+150	–52	202	0.90	7

phase, were of 20–50 $m^3 \cdot s^{-1}$, giving gross inflows of 140–200 $m^3 \cdot s^{-1}$ (*table IV*), compared with a potential flow maximum of 810 $m^3 \cdot s^{-1}$ (for H_{SAT} of 4–5 m).

3.4. Measured water characteristics

In Takapoto, we found salinities of about 38.5 p.s.u. (38.49 ± 0.09 p.s.u. in July 1999, 38.50 ± 0.06 p.s.u. in August 2000). During the second half of 2000, in the course of the dry season, the weekly monitoring showed a general increase (38.4 to 38.8 p.s.u.) interrupted by small dips (*figure 5*). These can be accounted for only when considering both rainfall and level variations (with an oceanic salinity of 36 p.s.u.). The first heavy rains (150 mm in one week) of late December 2000 (*figure 5*) can account for the observed salinity decrease.

In the set of other atoll lagoons, lagoon-averaged salinity Σ (from opportunity measurements sometimes spanning 2 years) was mostly about 36.5 p.s.u. ($35.9 < \Sigma < 36.8$ p.s.u.). A trend of increasing Σ with increasing T_{RAV} emerged when including Reka-Reka lagoon ($\Sigma = 37.3$ p.s.u.). The further inclusion of Taiaro, a practically closed lagoon ($\Sigma \geq 42.5$ p.s.u.), yielded a regression ($r^2 = 0.78$, $P < 0.01$ for $n = 13$), into which Takapoto fitted well (*figure 6*).

Total chlorophyll retained on GF/F filters, B_{tot}, showed concentrations ranging between 0.2 and 0.6 $\mu g \cdot L^{-1}$. No significant spatial difference appeared (0.33 ± 0.11 $\mu g \cdot L^{-1}$ in the NE, 0.50 ± 0.11 $\mu g \cdot L^{-1}$ in the SW). With GF/D filters, we found 0.18 ± 0.05 $\mu g \cdot L^{-1}$ in the NE, 0.28 ± 0.01 $\mu g \cdot L^{-1}$ in the SW. The ratio of chlorophyll concentrations retained on GF/D and GF/F filters, *D*/*F* (a size ratio), ranged between 0.3 and 0.7.

Light absorption by dissolved organic matter was rather uniform in Takapoto, with an average A_{254} of 0.96 m^{-1} (±0.11 m^{-1}) in the NE, and 1.12 ± 0.37 m^{-1} in the SW corner. These values correspond to dissolved organic carbon (DOC) concentrations of about 1 $mg \cdot L^{-1}$ (Pagès et al., 1997).

The two descriptors A_{254} and B_{tot} were not correlated in Takapoto itself, but were correlated (*figure 7*) when considering the whole set of 24 lagoons ($r^2 = 0.60$, $P < 0.01$). Moreover, data from lagoons around high islands (Raiatea and Mangareva) fitted into the trend, with some high values of A_{254} and especially of B_{tot} in narrow bays, while the closed atoll

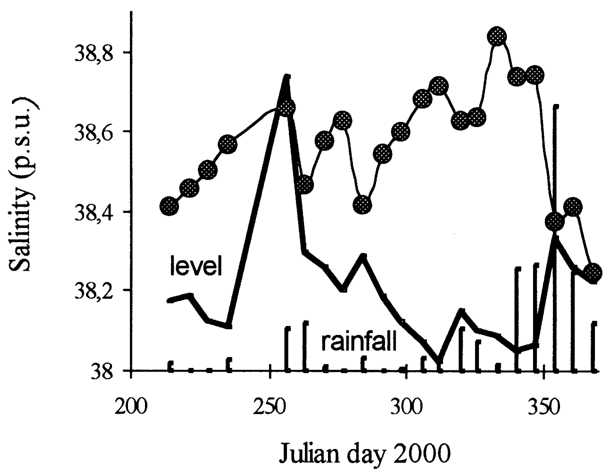

Figure 5. Variation of salinity in Takapoto Lagoon, from weekly sampling at two sites (error bars smaller than symbols) in late 2000. Lagoon level (range between 40 and 99 cm) and rainfall (summed for the week; range between zero and 222 mm) are shown for comparison.

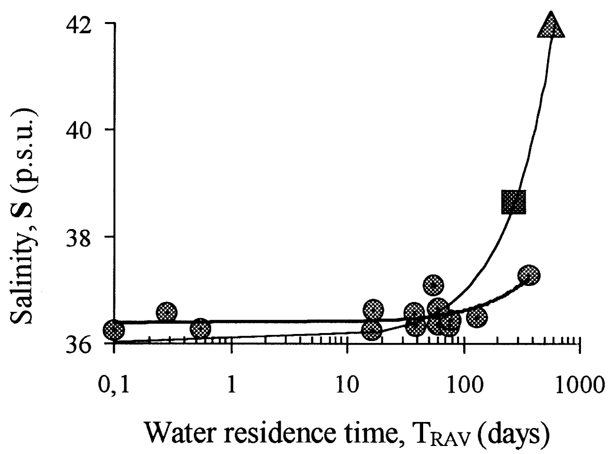

Figure 6. Variation of averaged salinity with average water residence time in different lagoons. The overall regression includes Taiaro (▲) but not Takapoto (■). The regression with 'normal' lagoons (● and light-shade curve) corresponds to a significant correlation.

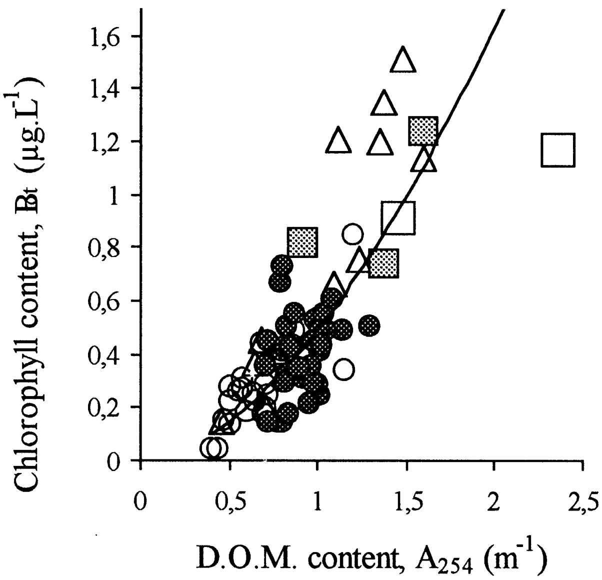

Figure 7. Variation of phytoplankton chlorophyll and dissolved organic matter concentrations in 'normal' lagoons (○), in lagoons under bloom conditions (▩, Hikueru and Takaroa), in semi-closed lagoons (□, Reka-Reka and Taiaro), and in lagoons and bays around high islands (△). Takapoto represents the upper limit of the 'normal' group.

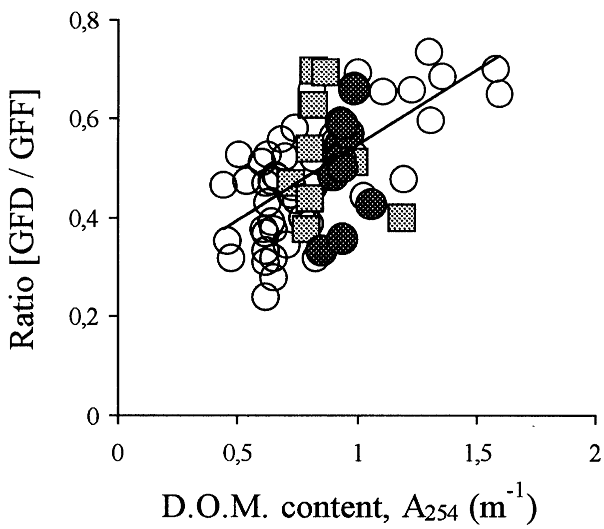

Figure 8. Variation of primary producer size with trophic state estimated by dissolved organic matter concentration. Chlorophyll-containing organisms retained on GF/D filters become less numerous, compared with the 'total' retained on GF/F filters, in oligotrophic waters.

lagoon of Taiaro showed higher dissolved organic matter concentrations. In the same way, the size ratio *D*/*F* was not correlated with A_{254} in Takapoto itself (*figure 8*) but the inclusion of other measurements, by

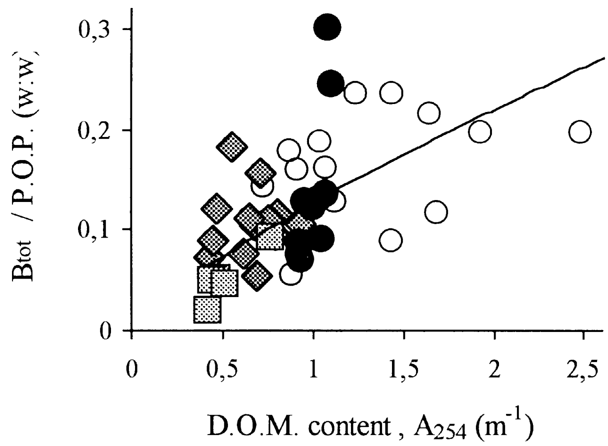

Figure 9. Variation of the ratio of chlorophyll to particulate organic phosphorus with the trophic state estimated by dissolved organic matter content. The trend is apparent when comparing the lagoon of Raiatea (■), the TypAtoll lagoons (◆, average by lagoon) and the lagoon of New Caledonia (○) with that of Takapoto (●). The correlation remains significant ($r^2 = 0.377$, $P < 0.01$) without the extreme data point at $A_{254} = 2.5$ m^{-1}, and despite the Takapoto outlier at B_{tot}/POP = 0.3.

broadening the range of situations, showed a general increase in the ratio *D*/*F* (i.e a higher proportion of 'large' chlorophyll-bearing cells) as dissolved organic matter increased ($r^2 = 0.25$, $P < 0.01$ for $n = 59$). Here again, data from high-island lagoons fitted into the trend.

We made some exploratory measurements of *POP* in view of a future study on seston. Concentrations in Takapoto ranged between 60 and 180 nmol·L^{-1}. These values agree with those found in the TypAtoll lagoons (40–200 nmol·L^{-1}; Charpy et al., 1997), in the lagoon of New Caledonia (Fichez et al., unpublished data), and with those we found in the lagoon of Raiatea in July 1999. The ratio of B_{tot} to *POP* (by weight) increased with increasing dissolved organic matter (*figure 9*). Again, the trend is not significant when only the data from Takapoto are considered, but becomes acceptable ($r^2 = 0.39$, $P < 0.01$ for $n = 45$) with the broader range of situations found when the other three series are included.

We found no correlation between salinity and biological variables (A_{254} and B_{tot}). It has already been noted that neither salinity nor water temperature has any effect on oyster growth rates in several lagoons including Takapoto.

4. DISCUSSION

4.1. Flushing rates

Compared with exchanges due to the tide, water input by wave overtopping is predominant, especially in the northern and central Tuamotu (where spring tides are ~ 0.3 m). We have already mentioned that local wind speed is a poor predictor of H_{SAT}.

The specific input flow rates measured on Takapoto (relative to wetted width, and not to reef edge length) were ≤ 0.5 $m^2 \cdot s^{-1}$, this value being plausible for the swell conditions we observed (H_{SAT} < 2 m). On other Tuamotu atolls, flow rates of up to 1.4 $m^2 \cdot s^{-1}$ have been found for H_{SAT} of 3.5 m. In this respect, the Takapoto reef face appears normal. Cross-reef flow rate values are found in the literature (Munk and Sargent, 1948; Atkinson et al., 1981; Hearn and Parker, 1988; Roberts et al., 1988; Prager, 1991) but comparisons are difficult, since several studies dealt with barrier reefs ('reef awash', von Arx, 1948), or considered flow rates relative to reef edge length (Lenhardt, 1991). Cross-reef current in a *hoa* on Moruroa (Tartinville et al., 2000) was ≤ 0.3 $m \cdot s^{-1}$ over 60 days, while we measured current speeds between 0.5 and 0.9 $m \cdot s^{-1}$ on Takapoto. Here again, Takapoto would appear normal, at least at this small scale.

For the entire lagoon and considering the Tuamotu atolls, total inflows (either potential flows or from field measurements), are low for the size of Takapoto. This, however, is to be expected considering the abnormally low aperture of this atoll when compared with several other Tuamotu atolls (see section 3.2), so that a normal minimum aperture would be about 3 km for Takapoto instead of the actual 0.1 km. Local plans regarding improving water renewal by blasting new openings through the reef could consider these numbers as an indication of the scale required for effectiveness.

4.2. Salinity and water residence time

All studies on Takapoto have found a hyperhaline lagoon (Sournia and Ricard, 1975, 1976; Magnier and Wauthy, 1976; Wrobel, 1997), with salinities mostly above 38 p.s.u. compared with ~ 36 p.s.u. in the surrounding ocean. Salinity would appear to be a good estimator of water residence time: for a closed basin of mean depth Z, under evaporation and rainfall rates E and R, salinity increases from S_o to S_t at time t according to the classical exponential relation: $S_t = S_o \times \exp\{[(E - R) / Z]\, t\}$ (e.g. Smith and Jokiel, 1978). Between August 1975 and December 1977, Guérédrat and Rougerie (1978) calculated that, apart from rainfall and evaporation, a permanent flushing of 50 $m^3 \cdot s^{-1}$ of oceanic water (compared with our $\Sigma\, Q_{AV}$ of 80 $m^3 \cdot s^{-1}$) was necessary to balance the salt budget. Our monitoring on a shorter time scale also showed that oceanic water inputs (deduced from lagoon level variations) must be taken into account. Moreover, an evaporative loss of 5 mm per day across the area of Takapoto Lagoon (81 km^2) represents 112 $m^3 \cdot s^{-1}$, i.e. about the average inflow across the reef. Determining the residence time for Takapoto from salinity evolution is then not straightforward.

In the set of 24 Tuamotu lagoons, salinity increased with computed average residence time, T_{RAV}. We have been dealing with averaged salinities, measured according to opportunity and which integrated the effects of several seasons. The correlation found between Σ and T_{RAV}, either in normal lagoons or in the whole range, then only stressed the existence of a common reaction of salinity to T_{RAV} among 24 lagoons.

The correlations found between T_{RAV} and salinity, chlorophyll concentration and dissolved organic matter content indicate that T_{RAV} allows a ranking of lagoons, which is mirrored by that derived from measured, actual water characteristics. The general aim set by Takeoka (1984, p. 319) would be met, but the absolute value of T_R is still debatable. We have found an average T_R of 268 days, with extreme values of 2700 days (7.5 years) and 27 days corresponding to $\Sigma\, Q_{min}$ and $\Sigma\, Q_{Max}$ respectively. Calculations of the residence time based either on salinity variations or on the ^{137}Cs deposition rate have yielded for Takapoto residence times ranging between 3.6 and 5.3 years, while total discharge through the *hoa* (obviously measured under very calm conditions) corresponded to a residence time of 6.7 years (reviewed in Delesalle and Sournia, 1992). On this latter point of *hoa* discharge, we noted (section 3.1) that low wave conditions during a field study appear highly probable. The low magnitude of flow rates (or current speeds) recorded by previous studies on Takapoto under differing (and often unspecified) wave climates (*table III*) is explained by the relationship between wave height and cross-reef flow (Gourlay, 1996a,b; Symonds et al., 1995) . A value for T_R (in any lagoon) is then meaningful for given simultaneous environmental conditions (swell, wind, etc). If an estimate of residence time better than an average T_R under average conditions is to be determined, long term monitoring and repeated measurements under varying conditions are necessary.

4.3. Residence time and biology

Our observations gave an average chlorophyll concentration (on GF/F filters) of 0.4 $\mu g \cdot L^{-1}$, which is comparable with previous measurements (Delesalle et al., 2001). Chlorophyll and dissolved organic matter contents were loosely related to each other inside Takapoto, and were well correlated in the set of 24 lagoons, either in normal situations (including Takapoto) or under moderate bloom conditions (*figure 7*). In atoll lagoons, dissolved organic matter is mainly produced by phytoplankton, either directly through exudation or indirectly through 'sloppy feeding'. The parallel increase of A_{254} and B_{tot} indicates that dissolved organic matter heterotrophic decomposition does not increase in proportion to dissolved organic matter concentration. Bacteria are relatively less active in rich waters, compared to autotrophs. Each lagoon would thus represent a stable state at a different level of trophy.

High chlorophyll concentration might result from higher nutrient loading. The low nutrient concentrations found in Takapoto (Sournia and Ricard, 1976; Sakka et al., 1999) are on a par with those found in the TypAtoll lagoons when considering only the inorganic forms (Dufour et al., 1999). Takapoto and the TypAtoll lagoons are also similar with regard to dissolved organic forms (*DON* ~ 75% of total dissolved N, *DOP* ~ 50% of total dissolved P. Dufour, personal communication). The growth kinetics of continuous culture reactors (under constant substrate concentration and variable dilution rate) are the simplest explanation for high B_{tot} values under long residence times (Furnas et al., 1990; Delesalle and Sournia, 1992). The major bloom in Hikueru lagoon in April–March 1994 (Adjeroud et al., 2001) occurred after periods of low wind and/or calm seas, underlining the effects of low energy hydrodynamics at the scale of 10^1–10^3 m, which contrast with those of high turbulence at a smaller scale (Baird and Atkinson, 1997; Thomas and Atkinson, 1997).

Since high biomasses are found under long residence times, lagoons with particularly low potential flows (relative to their volume) should be at higher risk of blooms – and Takapoto should be especially prone to blooms, which is not the case. Conditions of very low wave energy (or wind speed) are short lived (if frequent), and the time scale of biological reactions seldom fits into climate variability. The routine monitoring of between 7 and 12 atolls for the last three years has not been conclusive in this respect. Conversely, the lagoon of Takaroa, which has a relatively low minimum aperture, has shown biomass increases (up to 4 fold) with an abnormally high frequency (Prasil, unpublished data).

Chlorophyll concentration is a bulk estimator of biomass. The quantitative increase of B_{tot} with T_{RAV} is parallelled by qualitative changes. Lower values of size ratio *D*/*F* (section 3.4) in oligotrophic, low dissolved organic matter waters is consistent with the dominance of small picoplankton cells (Charpy and Blanchot, 1996, 1998; Delesalle et al., 2001). The increased abundance of *POP*, relative to B_{tot}, in oligotrophic waters is not due to a relaxation of P depletion but corresponds to an increase of non pigmented organisms. Oligotrophic waters harbour relatively more abundant heterotrophs (Dortch and Packard, 1989), and bacteria supersede autotrophs both in biomass and in activity. In confirmation of qualitative changes in the seston, pearl oysters have shown better growth rates in oligotrophic waters despite lower bulk biomass. In fact, the relatively poor growth of oysters in Takapoto Lagoon is the very reason for the planned improvement of water renewal we mentioned above.

5. CONCLUSION

The semi-closed lagoon of Takapoto, as described by early studies, could be considered anomalous by comparison with the few previously studied lagoons of French Polynesia (Guilcher et al., 1963; Michel et al., 1971). Its high biomass content, in particular, contrasted with nutrient concentrations that were lower (at least for the inorganic forms) than those of the surrounding oligotrophic ocean. The only 'logical' feature was high salinities explained by low water renewal rates.

We have had the rare opportunity of studying a large set of lagoons of differing characteristics with a typological approach. We have been able to detect trends that would not have emerged with a narrower range of situations. In particular, the wide range of residence times available with the set of 24 lagoons has led to varying characteristics in a series of 'natural laboratory' experiments in "large, somewhat leaky reactor[s]" (Smith and Jokiel, 1975). We have seen that continuous culture kinetics seem to apply. An atoll lagoon may also be viewed as "a lake in mid-ocean" (von Arx, 1948). With this point of view, the results of comparative limnology studies are not to be rejected (e.g. Søballe and Kimmel, 1987; Nürnberg, 1998). We could see that Takapoto Lagoon follows general trends that link water exchanges through the reef rim with lagoon water characteristics.

The few descriptors available during the PGRN program, and the circumstantial evidence provided by other variables, indicate that water renewal rate modifies the whole trophic web organisation. Assessing the role and importance of microheterotrophs and of mesozooplankton could confirm this (Delesalle et al., 2001).

Acknowledgements. This study was carried out in French Polynesia during two research programs. TypAtoll was organised and funded by IRD (previously ORSTOM), with financial help from PNRCO (*Programme national de recherche sur les écosystèmes coralliens*) and from the Government of French Polynesia, with the collaboration of the *Université française du Pacifique* and the *École pratique des hautes études*. PGRN (*Programme général de recherche sur la nacre*, General Research Program on Pearl Oyster) obtained the financial support of the Ministry for Education, Research and Technology, the Ministry for Overseas, and the Government of French Polynesia. Wave height data were gathered from a web site (R. Leben: www-ccar.colorado.edu/~ realtime / global_data_waves/wave.html). We gratefully acknowledge the constructive criticisms and remarks of two reviewers who struggled through a first draft of this paper, and the help of Hilary Todt with the English of a second version.

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