A MODEL OF THE RELATIONSHIP BETWEEN LIGHT AND PRIMARY PRODUCTION IN AN ATOLL LAGOON

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The Tikehau atoll (Tuamotu Archipelago, French Polynesia) is located at 14°S 148°W. Phytoplankton and sand microalgae are the most important primary producers of the lagoon. They were studied for 4 years.

The relationship between light energy and lagoonal primary production was measured by using the ^{14}C method for phytoplankton and O_2 method for phytobenthos. Incubations, carried out *in situ*, were made at different depths and light exposition times.

Irradiance was high and 17% of the light energy measured at the surface reached 25 m (lagoon average depth). Maxima of phytoplankton and phytobenthos productions occurred at low depths; there was therefore no photoinhibition of photosynthesis. Correlations between light energy and primary production were strong, especially for phytobenthos. Multiplicative linear regression models (production *vs* light) associated with an exponential linear regression model (light *vs* depth), allowed planktonic and benthic primary production to be predicted from the depth and the light energy received at the surface. The benthic primary production exceeded the phytoplanktonic production in the upper 18 m. The total primary production (benthos + plankton) was constant with depth and depended only on light energy at the surface. One Einstein received at the lagoon surface allowed the growth production of 14 mg of carbon (water column + sediments).

INTRODUCTION

The major factor determining the productivity of primary producers is their photosynthetic capacity defined as the saturation level of the productivity *vs* irradiance (Larkum, 1983). Raven *et al.* (1979) have suggested that the photosynthetic capacity of algae varies according to their ecological characteristics. Maximum photosynthetic capacity is rarely achieved in natural communities owing to the limiting factors (stirring, light intensity, temperature, nutrient supply, inorganic carbon supply and oxygen concentration).

Light-photosynthesis models have been proposed in the marine environment to estimate phytoplankton production (*e.g.* Jassby & Platt, 1976; Platt & Jassby, 1976) and photosynthetic efficiency was quantified by the calculation of quantum yield coefficients. However no model has been proposed for microphytobenthic production and, consequently, for the whole productivity of microphyte (plankton + benthos).

The purpose of this paper is to build a light-photosynthesis model for total microphyte communities of an atoll lagoon.

We have chosen the atoll of Tikehau as a study site since it can be considered, due to its geomorphology, as being representative of the 'open' atolls of the Tuamotu Archipelago (French Polynesia). Its lagoon surface is 400 km² with an average depth of 25 m (Lenhardt, 1987). The 25 km² of land are crossed by flat reef spillways linking the lagoon and ocean; one of which, westward located, makes a 200 m wide and 4 m deep passage. In general, oceanic waters go into the lagoon by the east and south-east spillways and out by the westward passage. Nutrient concentrations are low in the lagoon: 0·09 mmol NO_3 m⁻³ and 0·16 mmol PO_4 m⁻³ (Charpy-Roubaud & Charpy, 1990). Particulate organic matter is composed of 86% detritus (Charpy & Charpy-Roubaud, in preparation). The lagoon bottom is mainly composed of fine to very fine sand (Intes & Arnaudin, 1987) and presents an important bioturbation. The sand populations appeared to consist of diatoms, cyanobacteria and foraminifera; however, *Halophila* were commonly observed.

MATERIALS AND METHODS

Sampling stations

The stations investigated for primary production measurements were mainly in the southern part of the lagoon, in the immediate neighbourhood of the laboratory (Figure 1). Phytoplankton and phytobenthos biomass samples were taken in the whole lagoon. Phytoplankton was studied between 1983 and 1987 and microphytobenthos between 1985 and 1987.

Methods

Phytoplankton photosynthetic rate was determined using the ¹⁴C method of Steemann Nielsen (1952). *In situ* incubations were performed, in duplicate, between 1000 h and 1400 h in 300 ml borosilicate vials; total contents were filtered through a GF/F filter, then rinsed with 10 ml HCl (0·1N). Radioactivity measurements were made by liquid scintillation counting using an Aquasol-2 scintillator. Quench corrections were made using the external standard ratio. For each batch of incubations, contents of two vials filled with surface water were filtered two minutes after the ¹⁴C addition for the zero time blank (DPM_{to}); this DPM_{to} never rose above 2% of light-bottle counts but was subtracted from all productivity samples in accord with the recommendation of Morris *et al.* (1971). Dark-bottle counts were not subtracted from the light-bottle count as recommended by Legendre *et al.* (1983), but it never rose above 25% of the light-bottle counts. Phytoplankton production (PP) was calculated by the equation:

$$PP \ (\text{mg C m}^{-3}\text{h}^{-1}) = (DPM_{sample} - DPM_{to}) \ C \ (1/A^*) \ (1/dt) \qquad (1)$$

where C = concentration of CO_2 in the lagoon waters. We took the value 24 mg C-CO_2 m⁻³ (average of 12 analyses) for all the calculations. A^* = added activity: 4·4x10⁶ DPM for all ¹⁴C incubations; dt = incubation time (h).

Chlorophyll *a* (Chl *a*) was determined fluorometrically after extraction with 90% acetone using a glass-fibre filter (Whatman GF/F) (Yentsch & Menzel, 1963).
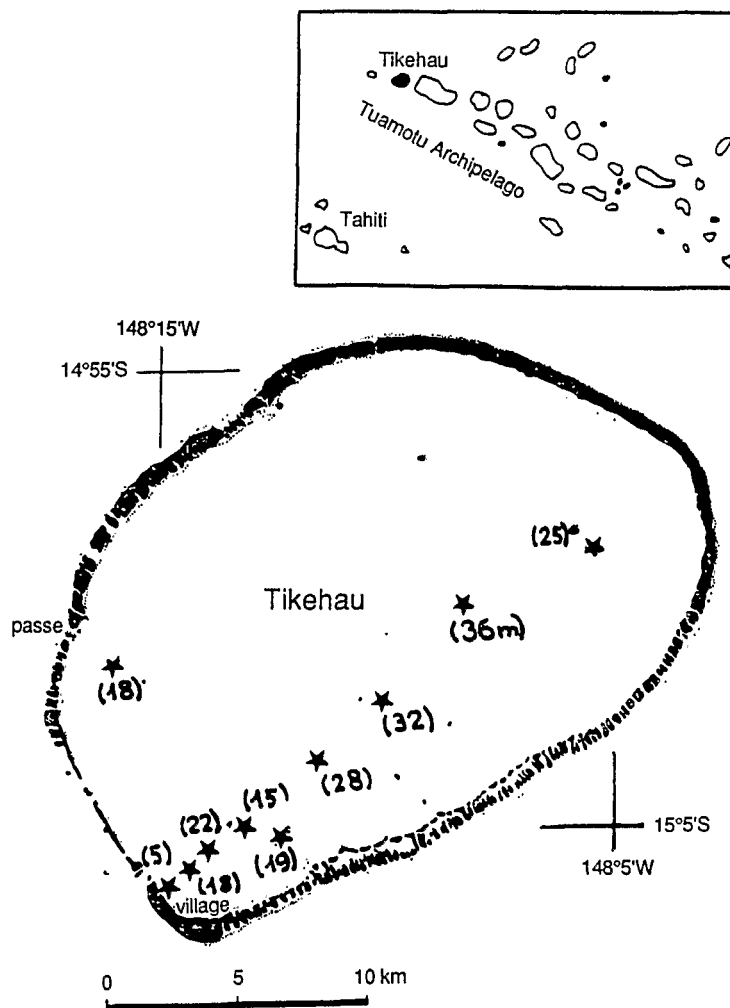
Figure 1. Station locations of *in situ* productivity measurements.

Phytobenthos production was determined by O_2 budgets, measured within clear and dark Plexiglass domes (285 cm^2, 4·2-5 l). For depths less than 12 m, we used a YSI probe fitted with a high sensitivity membrane, calibrated to 100% of O_2 saturation in H_2O saturated chamber. For larger depths, 120 ml of water was taken by a syringe in the domes at the beginning and the end of incubation and dissolved O_2 measured using the Winkler method. Stirring (stirrer of the YSI probe) took place within the dome during long time incubations (>4 h) to prevent the build-up of O_2 gradients. Reproducibility of results had been tested in a previous work (Charpy-Roubaud, 1986b).The production of O_2 (BP_{O2}) may be converted into the gross production of carbon (BP) by the equation of McCloskey *et al.* (1978):

$$BP = (BP_{O2}\ 0·375\ PQ) + (R\ 0·375\ RQ) \tag{2}$$

where R = respiration during daytime, PQ and RQ = photosynthetic and respiratory coefficients.

Microphytobenthos biomass was estimated by sediment Chl a concentration measurements in accordance with the procedure described by Plante-Cuny (1984). Sediment samples for chlorophyll measurements were obtained by SCUBA with a hand-corer of 2·7 cm inner diameter, from which 0·5-cm-thick slices were easily removed in the laboratory. Pigment extraction followed immediately in 90% acetone. Readings were made before and after acidification on a Turner 111 fluorometer, following the method of Yentsch & Menzel (1963). Charpy-Roubaud (1986a) observed chlorophyll down to a depth of 10 cm in the sediments of Tikehau; however below 0·5 cm, the level of light would be very low. Therefore, results are expressed as mg Chl a m^{-2} for the upper 0·5 cm of sediment.

Light energy (photosynthetically active radiation) was measured with a LI-COR solarimeter. The integration time chosen during incubation was 15 min. For daily light energy measurements, integration time was 24 h. In the water, light energy was measured with a LI-COR Model 185-A quantum meter fitted with a spherical probe.

RESULTS AND DISCUSSION

Light energy

Irradiance measurements were performed every day in 1986; therefore we present data only for this year. Light energy varied between 10 E m^{-2} d^{-1} during a southern winter cloudy day and 59 E m^{-2} d^{-1} during a southern summer sunny day (Figure 2).

Percentages of the light energy measured at the surface decreased with depth (Figure 3) with an exponential relationship:

$$\% \text{ of incident energy} = e^{(4\cdot45 - 0\cdot066\, depth)} \tag{3}$$

We observed that 17% of the surface light energy reached 25 m (average depth of the lagoon).
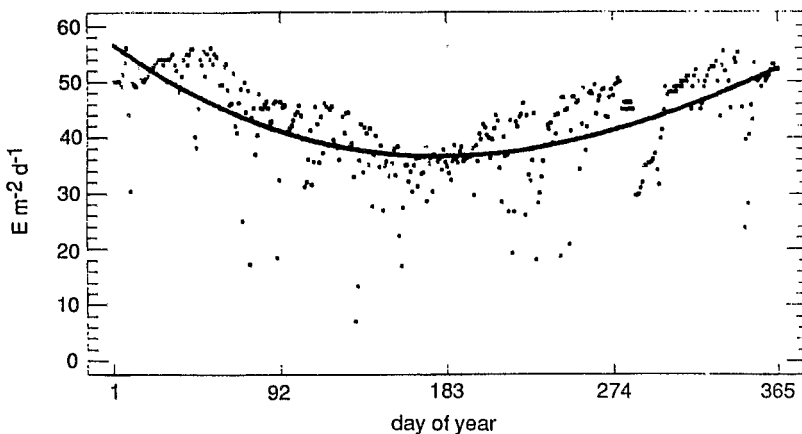

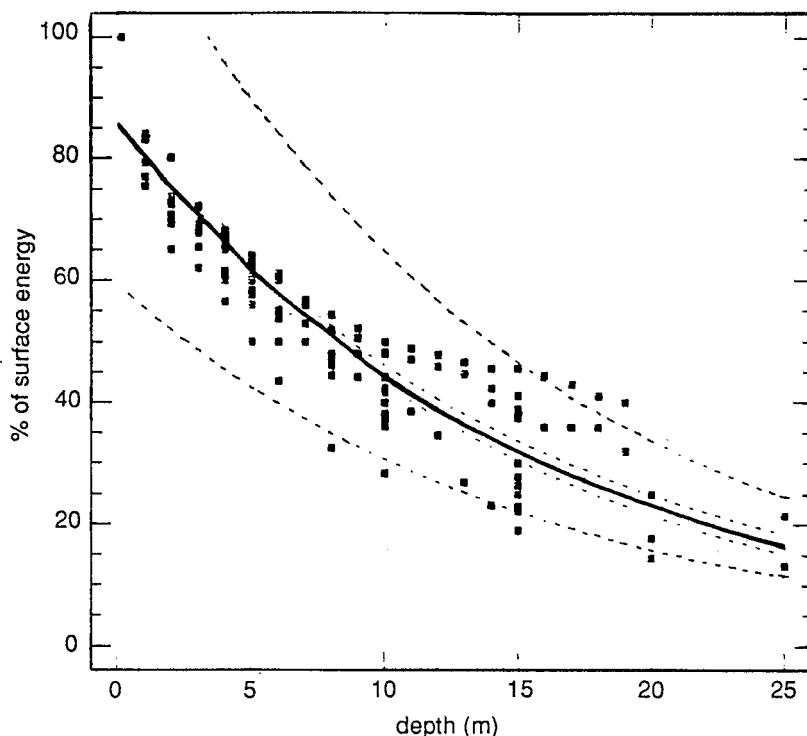Figure 2. Light energy measured in 1986 at the surface.

Figure 3. Regression of percentage of surface light energy on depth.

Relationship between phytoplankton production and light

Phytoplankton production (PP) and assimilation number (P_B) were clearly higher in the upper two metres than at other levels (Table 1). This lack of photoinhibition on phytoplankton production has already been observed in Takapoto (Sournia & Ricard, 1976) and Mataiva (Delesalle, 1985) Tuamotu atolls. Phytoplankton assemblages were dominated in summer by cells smaller than 5 μm (Charpy & Charpy-Roubaud, in preparation) with abundance of cyanobacteria (150,000 cells ml^{-1}) (Blanchot et al., 1989).

Table 1. *Phytoplankton production (PP) and assimilation number (P_B) averages and confidence intervals (P=95%) in relation to depth*

depth (m)	n	PP mg C $m^{-3}h^{-1}$	P_B mg C (mg Chl a h^{-1})$^{-1}$
0 - 2	52	3.92 ± 1.02	21.1 ± 7.5
2 - 5	22	2.27 ± 0.67	13.0 ± 5.1
5 - 10	42	2.68 ± 1.33	13.5 ± 4.9
10 - 15	21	2.00 ± 0.72	11.2 ± 5.6
15 - 20	7	1.17 ± 1.15	4.7 ± 3.5
20 - 24	2	0.54	4.2

Therefore, the picoplankton of Tikehau appeared to be very well adapted to higher energy levels contrary to the consensus that picoplankton is more adapted to low light conditions than the larger phytoplankton cells (Joint & Pomeroy, 1986); however, Joint (1989), concludes that there appears to be very little evidence to support the hypothesis that the response of picoplankton in natural assemblages to light is any different from that of other phytoplankton. Legendre *et al.* (1988) observed, in oceanic waters close to Moorea Island (French Polynesia), that the maximum assimilation number was lower in the <2 m fraction than in other size fractions. These authors observed the contrary for plankton above the barrier reef.

Phytoplankton production (PP) is correlated with light energy (Eh) (Figure 4) with a correlation coefficient equal to 0·38 (n = 43). PP may be predicted, with a standard error of 0·6 mg C m^{-3} h^{-1}, by using the multiplicative relation:

$$PP \ (\text{mg C m}^{-3}\text{h}^{-1}) = e^{\ 0.254} \ Eh^{0.39} \ (\text{E m}^{-2}\text{h}^{-1}) \eqno(4)$$
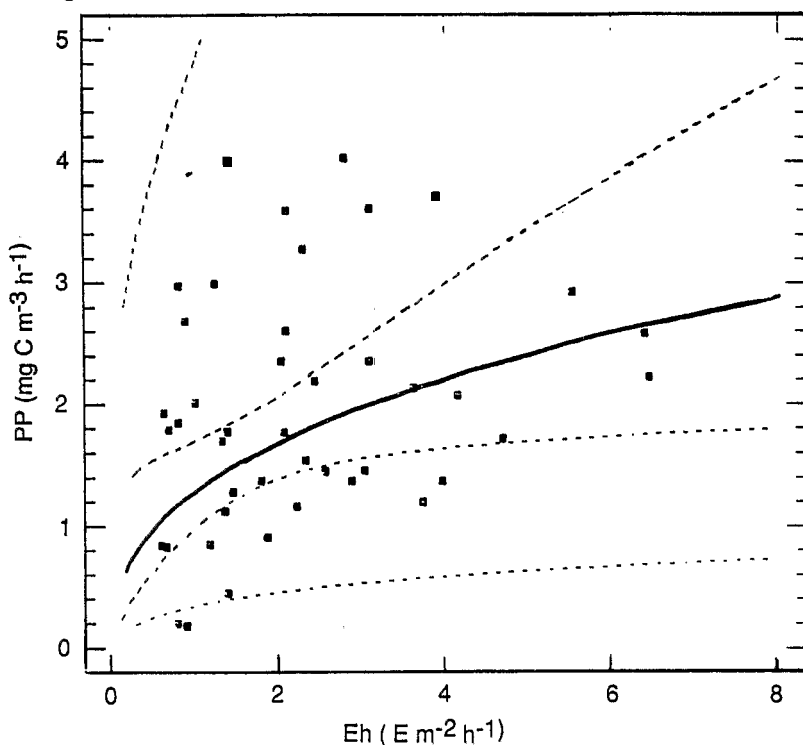

Figure 4. Regression of phytoplankton production (PP) on light energy (Eh).

Relationship between microphytobenthos production and light

In order to observe the influence of light energy on net oxygen production, measurements of O_2 budgets were performed inside enclosed domes set to low depth (Charpy-Roubaud, 1988). We observed a strong relation between O_2 production and light energy (Figure 5) without photoinhibition at natural energy levels. The high correlation between O_2 production and light energy (R=0·67, n=69) allows us to estimate daily

production (BP_{dly}) using incubations of short duration by the equation:

$$BP_{dly} \ (g \ O_2 \ m^{-2} \ d^{-1}) = BP_{(t-to)} \ Eds \ E_{(t-to)}^{-1} \tag{5}$$

where $BP_{(t-to)}$ = net production during the incubation period t-to; Eds (E $m^{-2} d^{-1}$) = daily energy measured at the surface; $E_{(t-to)}$ = energy measured at the surface during the incubation.

Fifty measurements of short duration (2-6 h) were made at different stations and times and BP_{dly} calculated with equation (5). Phytobenthos biomass and production were clearly higher at low depth (Figure 6). The average Chl a concentration was 9·6 mg m^{-2} below 3 m and 17 mg m^{-2} in the upper 3 m. Sournia (1976), in the sands of Takapoto
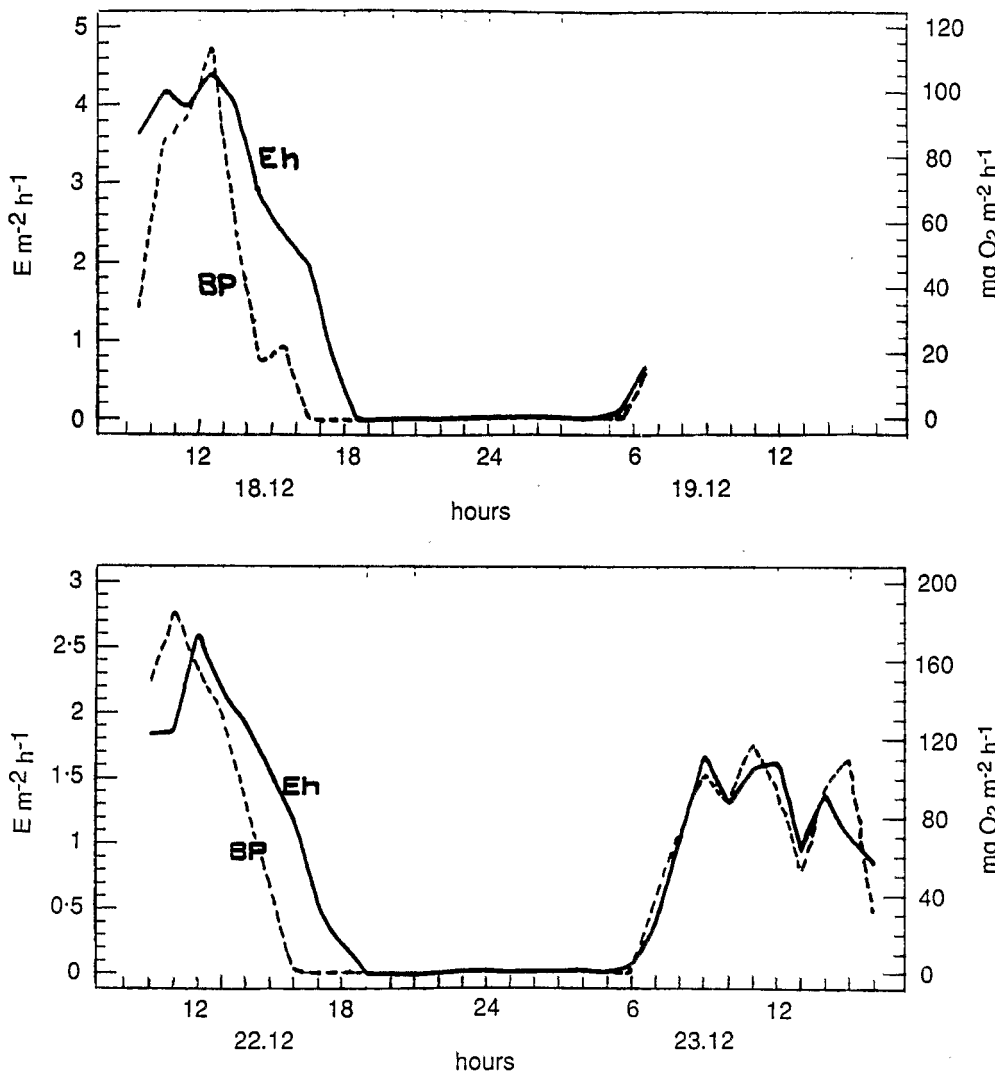

Figure 5. Light energy (Eh) and benthic productivity (BP) continuously measured at 2·3 m (A) and 6 m (B).

atoll, observed Chl *a* concentration five times higher between 0 and 1 m depth than between 10 and 17 m depth. The average O_2 production that we observed in the upper 3 m ($1 \cdot 2 \pm 0 \cdot 3$ g O_2 m^{-2} d^{-1}) was in the lowest part of the O_2 production range calculated from results given by Sournia (1976) for depths between 0 and 1 m (hourly production x 10 h = $1 \cdot 1$-$3 \cdot 5$ g O_2 m^{-2} d^{-1}).

Oxygen production measured during continuous experiments and short time incubations, were converted into carbon growth production using equation (2). Because of the fact that the PQ and RQ of the microphyte communities of Tikehau lagoon have not been experimentally determined, we use a PQ and RQ of 1. The average respiration rate was: R = 31 ± 7 mg O_2 m^{-2} h^{-1}. Benthic production and (BP) (Figure 7) may be predicted
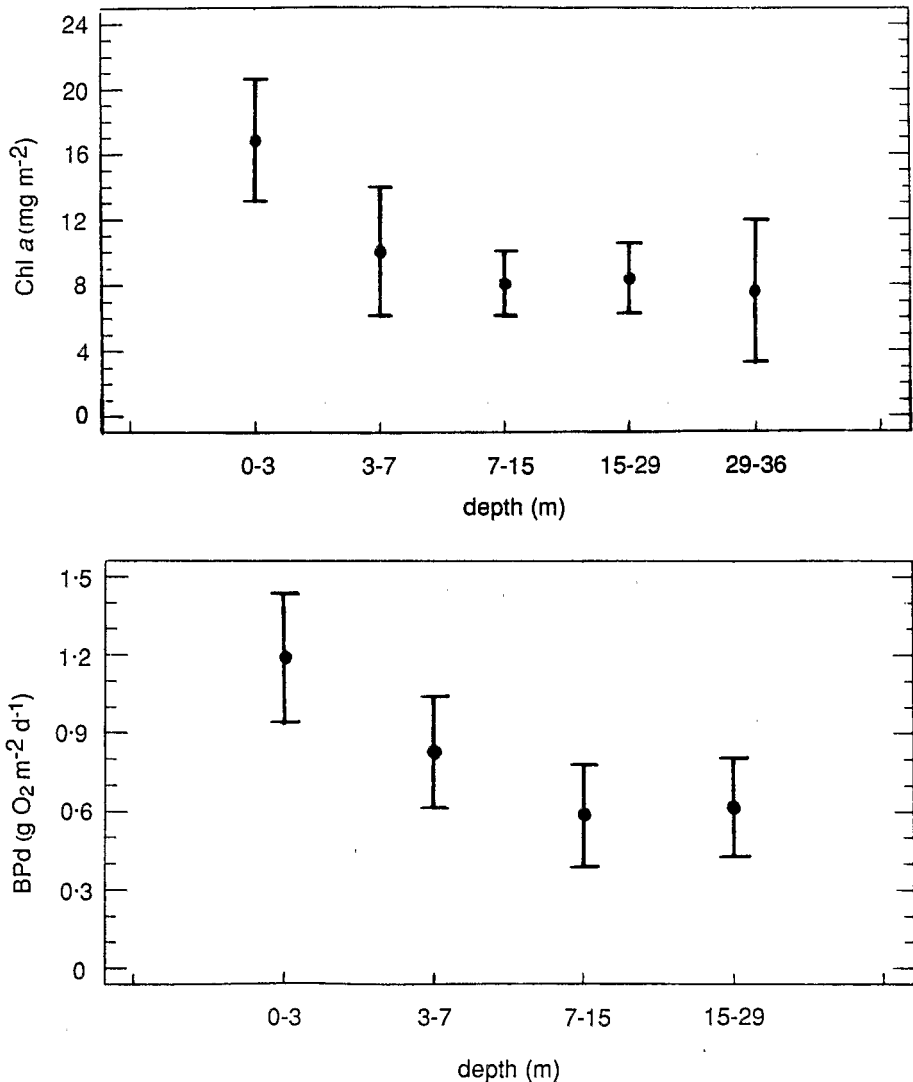

Figure 6. Benthic biomass and daily O_2 production (BPd) averages *vs* depth.

by using the regression model (R=0·66, n=179):

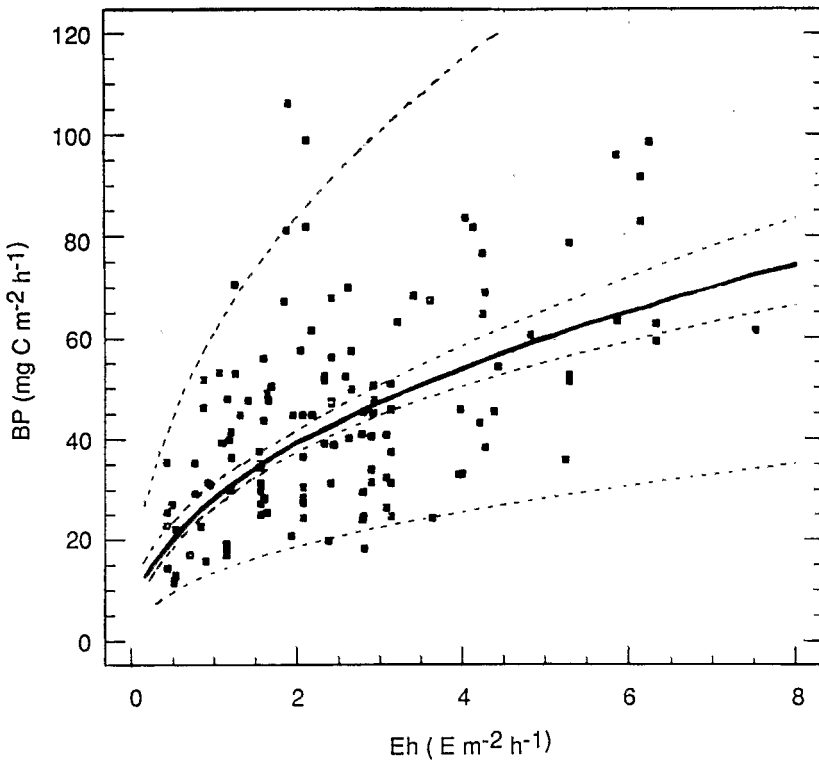$$BP \ (mg \ C \ m^{-2} \ h^{-1}) = e^{3 \cdot 36} \ Eh^{0 \cdot 454} \tag{6}$$

Figure 7. Regression of benthic production (BP) on light energy (Eh).

Benthic vs planktonic productivity

Phytoplankton production per cubic metre may be converted into production per square metre by using the equation:

$$PP_d = \int_{z=0}^{z=d} PP_z \tag{7}$$

where PP_d (mg C m^{-2} h^{-1}) = production at depth d; PP_z (mg C m^{-3} h^{-1}) = production at depth z.

Using equation (3) and (4), we obtain the final equation:

$$PP_d = \int_{z=0}^{z=d} e^{0.254} \left(e^{(4.45-0.06 z)} E_{hs} /100 \right)^{0.39} \tag{8}$$

where Ehs (E m^{-2} h^{-1}) = light energy at the surface.

Similarly, we can calculate the phytobenthos production at the depth d (BP_d) using equations (3) and (6):

$$BP_d = e^{3.366} (e^{(4.45-0.06 d)} Ehs / 100)^{0.454} \tag{9}$$

Planktonic and benthic production were calculated at depths between 0 and 36 m (maximum depth of the lagoon) for different Ehs values observed in natural conditions (1-8 E m^{-2}h^{-1}) (Figure 8). Phytobenthos production exceeded phytoplankton production in the upper 18 m. In the literature, there have been few attempts to evaluate what may be called the 'equivalent depth' because benthic measurements become rather scarce at depth. No generalisation can be made at this stage; equivalent depths of 2-40 m have been obtained (see review Charpy-Roubaud & Sournia, 1990). However, the estimated relative contribution of the benthos to total productivity is sensitive to the value of PQ; its actual value varies quite considerably (de Visscher, 1983).
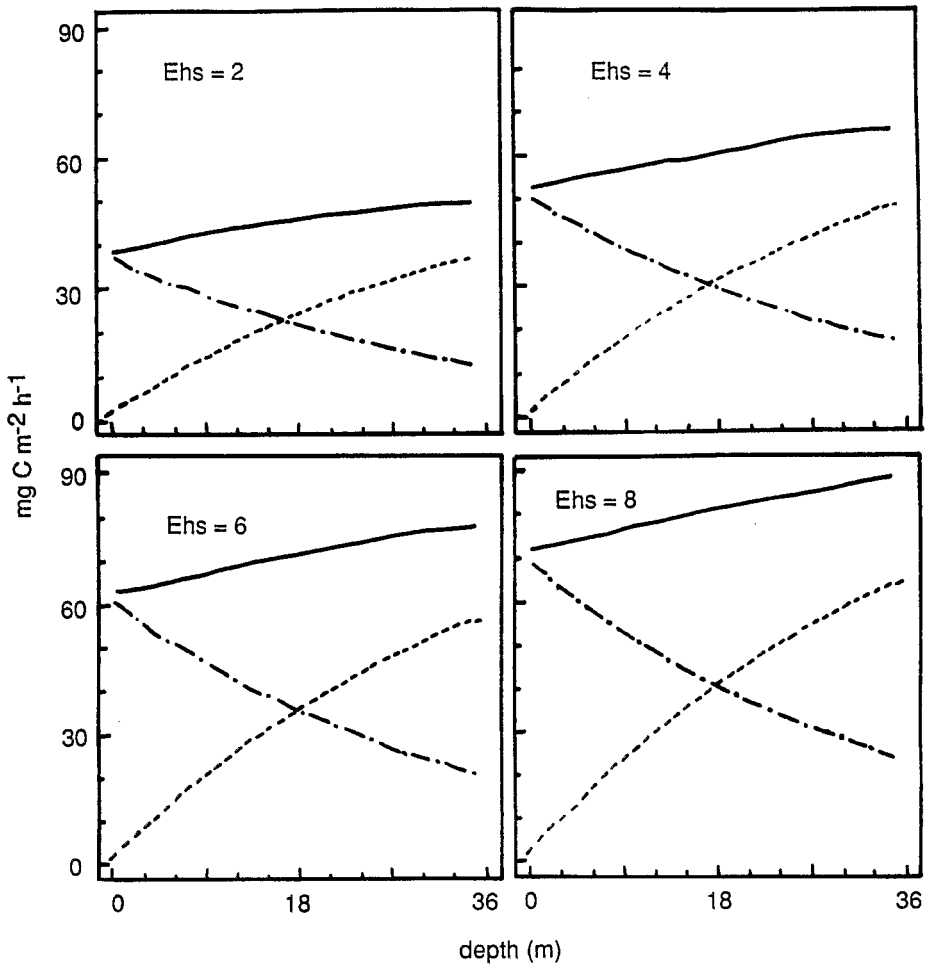

Figure 8. Predicted phytoplanktonic production (- - -), phytobenthic production (- · - · -) and total production (——) for different surface light energy levels (Ehs: E m^{-2}h^{-1}).

The total primary production (PT) was relatively constant with depth and depended only on the light energy at the surface. Therefore, we obtained an average PT for each value of Ehs, correlated with Ehs (R=0·99, n=8). PT and Ehs were linked by the relation:

$$PT = 6\cdot5 \; Ehs + 31\cdot5 \tag{10}$$

Therefore, daily total production (PT_{dly}) may be calculated, assuming a sun time of 10 h by the equation:

$$PT_{dly} \; (mg \; C \; m^{-2} \, d^{-1}) = 6\cdot5 \; Eds + 315 \tag{11}$$

where Eds (E $m^{-2} d^{-1}$) = daily light energy at the surface.

The PT_{dly} value for Eds=0 is equal to 315 mg C $m^{-2} d^{-1}$; it may be interpreted as the respiration in the water column and sediments. Daily light energy data obtained in 1986 may be converted into daily primary production using equation (11). Monthly averages of PT_{dly} are plotted in Figure 9. If we sum daily light energy and production, we observe that the lagoon received, in 1986, at the surface, 15,550 E m^{-2} (Eys) and that the water column and sediments produced 216,709 mg C m^{-2} (PT_{yly}). A preliminary estimation of the average Tikehau lagoonal primary production was made based on the depth/production relationship (using short time incubations) and bathymetric edge
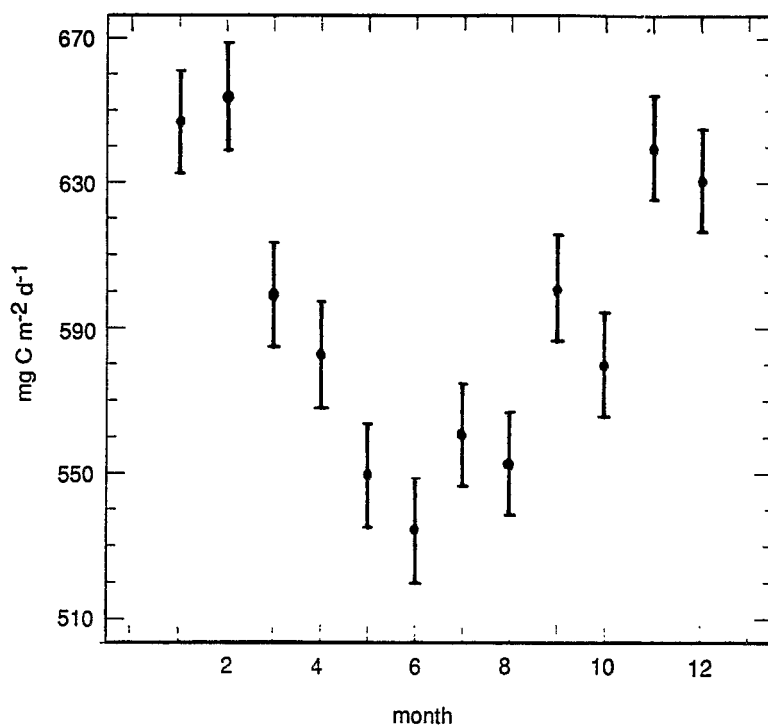

Figure 9. Monthly averages and confidence intervals (P=95%) of predicted total primary production (plankton + benthos) in 1986.

surfaces (Charpy-Roubaud, 1988). This first estimation (0.69 mg C m^{-2} d^{-1}) is not very different from the average daily production calculated in 1986 with our model: 0.59 mg C m^{-2} d^{-1}.

The photosynthetic efficiency of the lagoonal communities may be estimated by the ratios productivity/biomass (P_B) and productivity/energy (P_E).

The average assimilation number was:

$$P_B = (PT_{yly}/3650)/(\text{Chl } a_{pk}+\text{Chl } a_{be}) = 4.2 \text{ mg C mg}^{-1} \text{ h}^{-1} \tag{12}$$

where Chl-a_{pk} = average plankton Chl a = 4.5 mg m^{-2} (25 m depth); Chl-a_{be} = average benthos Chl a = 9.6 mg m^{-2}; 1 mg Chl a allows an hourly growth production of 4.2 mg carbon.

The average P_E may be estimated by the relationship:

$$P_E = PT_{yly}/Eys = 14 \text{ mg C E}^{-1} \tag{13}$$

One Einstein at the surface of the lagoon allows the growth production of 14 mg of organic carbon in the water column and sediments.

CONCLUSIONS

The importance of benthic microphytes in coastal ecosystems in the total primary production was demonstrated.

The Tikehau lagoonal communities of primary producers appeared to be very well adapted to high irradiance.

Our light-photosynthesis model, which takes into account both benthic and planktonic communities, appears to be suitable for predicting Tikehau lagoonal primary production; it would be important to test its validity in other Tuamotu atolls and coral reef areas.

REFERENCES

Blanchot, J., Charpy, L. & Le Borgne, R., 1989. Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu Archipelago). *Marine Biology*, **102**, 329-339.

Charpy-Roubaud, C.J., 1986a. Le microphytobenthos. I. Biomasse (premiers résultats). *Notes et Documents. ORSTOM Tahiti* (sér. Océanographie), **28**, 1-51.

Charpy-Roubaud, C.J., 1986b. Le microphytobenthos. II. Production primaire (premiers résultats). *Notes et Documents. ORSTOM Tahiti* (sér. Océanographie), **28**, 52-81.

Charpy-Roubaud, C.J., 1988. Production primaire des fonds meubles du lagon de Tikehau (Atoll des Tuamotu, Polynésie Française). *Oceanologica Acta*, **11**, 241-248.

Charpy-Roubaud, C.J. & Charpy, L. 1990. Bilans de l'azote et du phosphore dans un atoll ouvert du Pacifique Central (Tikehau, Tuamotu, Polynésie Française). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences* (sér. III), **310** (5), 163-167.

Charpy-Roubaud, C.J. & Sournia, A., 1990. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. *Marine Food Web*, in press.

Delesalle, B., 1985. Environmental survey of Mataiva Atoll, Tuamotu Archipelago French Polynesia. *Atoll Research Bulletin*, no. 286, 41 pp.

de Visscher, P. 1983. On PQ values. *Hydrobiological Bulletin*, **17**(1), 29-51.

Intes, A. & Arnaudin, H., 1987. Esquisse sédimentologique du lagon de Tikehau. *Notes et Documents. ORSTOM Tahiti* (sér. Océanographie), **35**, 71-100.

Jassby, A.D. & Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnology and Oceanography*, **21**, 540-547.

Joint, I.R., 1990. Does the response of picoplankton to light differ from that of other phytoplankton? In *Light and Life in the Sea*. (ed. M. Whitfield *et al.*), pp. 105-114. Cambridge: Cambridge University Press.

Joint, I.R. & Pomeroy, A.J., 1986. Photosynthetic characteristics of nanoplankton and picoplankton from the surface mixed layer. *Marine Biology*, **92**, 465-474.

Larkum, A.W.D., 1983. The primary productivity of plant communities on coral reefs. In *Perspectives on Coral Reefs* (ed. D.J. Barnes), pp. 221-230. [Australian Institute of Marine Science Contribution, 200.]

Le Borgne, R.P., Blanchot, J. & Charpy, L., 1989. Zooplankton of Tikehau atoll (Tuamotu Archipelago) and its relationship to particulate matter. *Marine Biology*, **102**, 341-353.

Legendre, L., Demers, S., Yentsch, C.M. & Yentsch, C.S., 1983. The ^{14}C method: patterns of dark CO_2 fixation and DCMU correction to replace the dark bottle. *Limnology and Oceanography*, **28**, 996-1003.

Legendre, L., Demers, S., Delesalle, B. & Harnois, C., 1988. Biomass and photosynthetic activity of phototropic picoplankton in coral reef waters (Moorea Island, French Polynesia). *Marine Ecology - Progress Series*, **47**, 153-160.

Lenhardt, X., 1987. Etude bathymetrique du lagon de l'atoll de Tikehau. *Notes et Documents. ORSTOM Tahiti* (sér. Océanographie), **35**, 53-70.

McCloskey, L.R., Wethey, D.S. & Porter, J.W., 1978. Measurement and interpretation of photosynthesis and respiration. *Monographs on Oceanographic Methodology*, **5**, 379-396.

Morris, I.C., Yentsch, C.M. & Yentsch, C.S., 1971. Relationship between light CO_2 fixation by marine algae. *Limnology and Oceanography*, **16**, 854-858.

Plante-Cuny, M.-R., 1984. Le microphytobenthos et son rôle à l'échelon primaire dans le milieu marin. *Oceanis*, **10**, 417-427.

Platt, T. & Jassby, A.D., 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. *Journal of Phycology*, **12**, 421-430.

Raven, J.A., Smith, F.A. & Glidewell, S.M., 1979. Photosynthetic capacities and biological strategies of giant-celled and small-celled macro-algae. *New Phytologist*, **83**, 299-309.

Sournia, A., 1976. Primary production of the lagoon of an atoll and the role of foraminiferan symbionts. *Marine Biology*, **37**, 29-32.

Sournia, A. & Ricard, M., 1976. Données sur l'hydrologie et la productivité du lagon d'un atoll fermé (Takapoto, Iles Tuamotu). *Vie et Milieu*, **26**, 243-279.

Steemann Nielsen, E., 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *Journal du Conseil*, **18**, 117-140.

Yentsch, C.S. and Menzel, D.W., 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Research*, **10**, 221-231.