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# Distribution and biomass of microphytes measured by benthic chlorophyll *a* in a tropical lagoon (New Caledonia, South Pacific)

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## Abstract

The microphytes biomass, measured as spectrophotometric concentrations of chlorophyll *a* in acetonic extracts, was studied at 120 randomly sampled stations in the south-western lagoon of New Caledonia (South West Pacific). The mean concentrations of pigments in the top centimetre of sediment (0–1 cm) were found to be 47.2 mg $m^{-2}$ (s.e. 1.2) for chlorophyll *a* and 78.4 mg $m^{-2}$ (s.e. 1.4) for phaeopigments. Small-scale, spatial scale and temporal scale distributions were heterogeneous. The spatial distribution of benthic chlorophyll *a* is affected by a combination of several parameters such as depth (and therefore light), sediment type and macrophyte interactions. Chlorophyll *a* maxima were found close to the reef on coarse white and well oxygenated sediment, whereas phaeopigment maxima existed close to the coast and were associated with fine sediment and detrital areas. Temporal variations were observed. An attempt to express the benthic chlorophyll *a* biomass as organic carbon was made using the C / Chl *a* ratios. This resulted in the benthic microflora trophic compartment being assessed at 2.4 gC $m^{-2}$. From the trophic level point of view, the primary producers, including micro and macrophytobenthos, dominate the system in terms of carbon biomass with 7.6 gC $m^{-2}$.

## Introduction

Microscopic algae living in sediments of all particle sizes are used as food by a range of species from several trophic groups as deposit swallowers or surface deposit feeders. The primary production of the microphytobenthos present in the surface sediment layer may be large, and generates a quantity of energy that is readily available to the food web (Moriarty et al., 1985). Much research has been done on microphytobenthic primary production over the full range of latitudes (Colijn & de Jonge, 1984; Plante-Cuny, 1984; Moncreiff et al., 1992). Chlorophyll *a* concentration in surface sediments can be used as an indirect measurement of the autotrophic biomass of benthic microflora (Wetzel & Westlake, 1969) as chlorophyll *a*, considered as 'functional chlorophyll' (Wetzel, 1964), corresponds to living phytal material and phaeopigments originate mainly from various detrital plant material or senescent cells (Plante et al., 1986). Several authors have shown that the microphytobenthic biomass thus measured can provide an useful index of potential production (Colijn & Venekamp, 1977; Plante-Cuny, 1978; Shaffer & Onuf, 1983; de Jonge & Colijn, 1994).

The aim of the present study was to examine the biomass and distribution of microphytobenthos in a New Caledonian lagoon in order to better understand the importance of these primary producers within the entire lagoon system. The study of the benthic microflora on the soft bottoms of the south-western lagoon of New Caledonia formed part of a larger research programme concerned with a compartmental analysis of the food web. Earlier work on the macrobenthos of the South West lagoon led to the identification of a number of compartments (primary producers, suspension feeders, deposit feeders, carnivores) and to the assessment of their biomass in terms of carbon (Chardy & Clavier, 1988a). A preliminary model for the functioning of the lagoon was then pro-

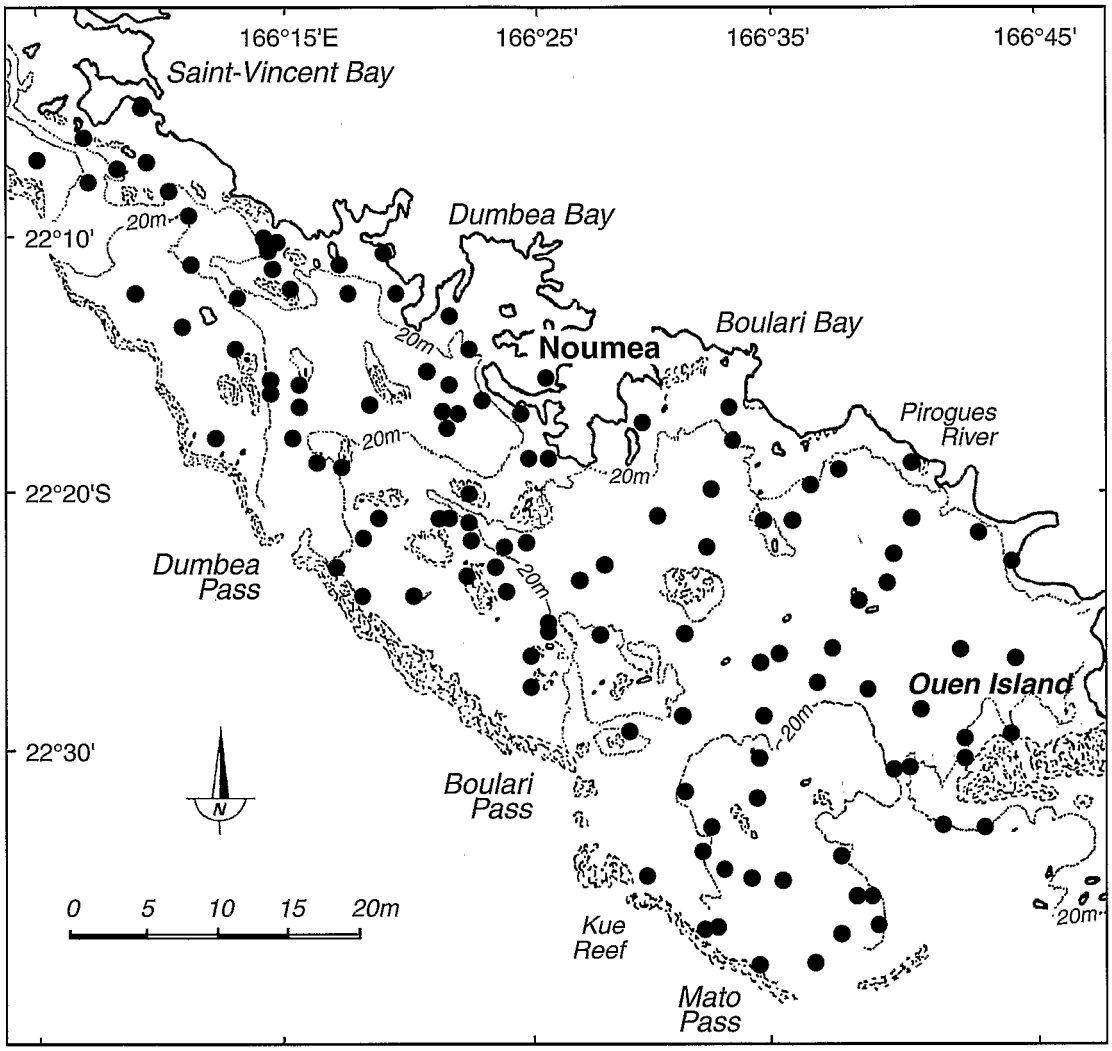


*Figure 1.* Location of the sampling sites.

posed (Chardy & Clavier, 1988b). Such a model can only input biomass values expressed in terms of carbon. In the present paper an attempt has been made to estimate microbenthic chlorophyll *a* in terms of carbon.

## Materials and methods

### *Study area*

The study area covers 2066 km$^2$ within the south-western lagoon of New Caledonia (South West Pacific, 22° S 166° E), extending, north-west to south-east, from St Vincent Bay to a line joining Ouen Island and Mato Pass (Figure 1). The trade winds, blowing from south-east to north-west, are dominant during most of the year. The amplitude of the diurnal tide is 0.80 m and the hydrodynamics of the area are not well known.

In the absence of any preliminary data on the benthic microflora, 120 stations were randomly chosen in the study area. The stations were sampled once between June 1989 and June 1990 (Figure 1). Their location was pinpointed to within 0.1 nautical miles in both latitude and longitude. All stations were located in the sublittoral zone between 4 and 36 m depth, the average depth being 19 m. The work was performed aboard RV 'Dawa'.

*Sampling and analysis*

At each station five sediment core samples (5.31 $cm^2$ in cross-section) were collected by divers, on one occasion only, within a 1 $m^2$ area in order to obtain a mean value. The cores were immediately sliced into 4 sections for later determination of the distribution of chloropigments over the thickness of the sediment, the slices representing the 0–1, 1–2, 2–4 and 4–6 cm layers. The samples were then frozen and stored in darkness while transported to the laboratory where they were freeze-dried. Pigment contents were extracted in 90% acetone (20 mL) over a period of 18–24 h in a refrigerator (Garrigue & Di Matteo, 1991). During the extraction, the sediment samples were occasionally shaken. The supernatants were subsequently filtered through a Millipore Prefilter and a Whatman GF/C glass-fibre filter in order to eliminate the suspended particles. The absorbance of the acetonic extract was measured at specific wavelengths (750 and 665 nm) with a Jobin Yvon Hitachi model 100-60 double beam spectrophotometer using 1 cm glass cuvettes before and after acidification of the extracts with HCl 0.5 N to a final concentration of $3.10^{-3}$ M/L (Holm-Hansen & Riemann, 1978). These values were used to calculate chlorophyll *a* (Chl *a*) and phaeopigment concentrations using the formulae by Lorenzen (1967). Pigment concentrations were reported as mg of pigments per square metre for the top centimeter of sediment. To get a good estimate of the biomass, only the first centimetre was used, as the top 0.5 cm leads to underestimating the biomass (de Jonge & Colijn, 1994). The 2–4 and 4–6 cm layers were corrected by halving the measures to account for the greater thickness of these layers (Garrigue & Di Matteo, 1991).

Various environmental parameters were measured at each station to provide a basis for interpreting the distribution of the benthic chlorophyll *a*. Depth (Depth) was measured in metres; distance (Dist) from shore was expressed in nautical miles. Macrophyte biomass, including seagrass and seaweeds (Macrophyte Afdw), was calculated and expressed as grams of Afdw $m^{-2}$ (Garrigue, 1995). Sediments were hand-collected by scraping for granulometric analysis, then particle size-fractions were determined according to the procedure of Folk & Ward (1957). Percentages of mud (%Mud) and of fine and very fine sands (%Fvfs) were calculated, along with the mean size (Ms), sorting (Df), standard deviation (Si), skewness (Ski) and kurtosis (Kg) which are expressed in phi ($-\log_{10} \times$ (mm) / $\log_{10}$ (2)) units.

*Data analysis*

Data analyses were performed on measurements for the upper centimetre of sediment, with the exception of vertical distribution where the whole sediment layer sampled (0–6 cm) was considered. Forward stepwise multilinear regressions were performed to determine the importance of environmental parameters (Depth, Dist,%Mud,%Fvfs, Ms, Si, Df, Ski, Kg, Macrophyte Afdw) in explaining the spatial distribution of chloropigments in the top centimetre of sediment. Homogeneity of variances was checked then ANOVA were performed first on data grouped by slices of sediment in order to estimate the distribution of pigments in the sedimentary column then on data grouped by month to investigate temporal variation of the biomass. *A posteriori* LSD tests were used to compare values for significant ANOVA results. Statistical analyses were carried out using SAS (SAS 1988) and STATISTICA software.

## Results

Coefficients of variation among replicate samples for each station varied from 8 to 92% for Chl *a* and from 4 to 65% for phaeopigment concentrations. No relationship could be established between the coefficients of variation and the physical (Depth, Dist) or sedimentological parameters of each station.

The mass of pigment in the top centimetre of sediment varied from 3 to 206 mg $m^{-2}$ ($N$ = 120; mean: 47.2; s.e.: 1.2; CV: 60%) for Chl *a*, and from 19 to 245 mg $m^{-2}$ ($N$ = 120; mean: 78.4; s.e.: 1.4; CV: 42%) for phaeopigments (Table 1). The distribution of Chl *a* followed a gradient from land to reef (Figure 2). Chl *a* concentration was lowest opposite the mouth of the Pirogues River and facing the reef passes (Figure 2), where the quantity of pigment was less than

*Table 1.* Concentrations (mean ± s.e.) of chloropigments within the different sediment layers ($N$: number of cores analysed)

| Layers (cm) | $N$ | Chlorophyll *a* (mg $m^{-2}$) (1 cm thickness) | Phaeopigments (mg $m^{-2}$) (1 cm thickness) |
|---|---|---|---|
| 0–1 | 594 | 47.17 ± 1.16 | 78.41 ± 1.36 |
| 1–2 | 319 | 24.23 ± 0.98 | 57.84 ± 1.37 |
| 2–4 | 270 | 10.01 ± 0.60 | 36.28 ± 0.91 |
| 4–6 | 120 | 4.11 ± 0.37 | 33.61 ± 1.23 |

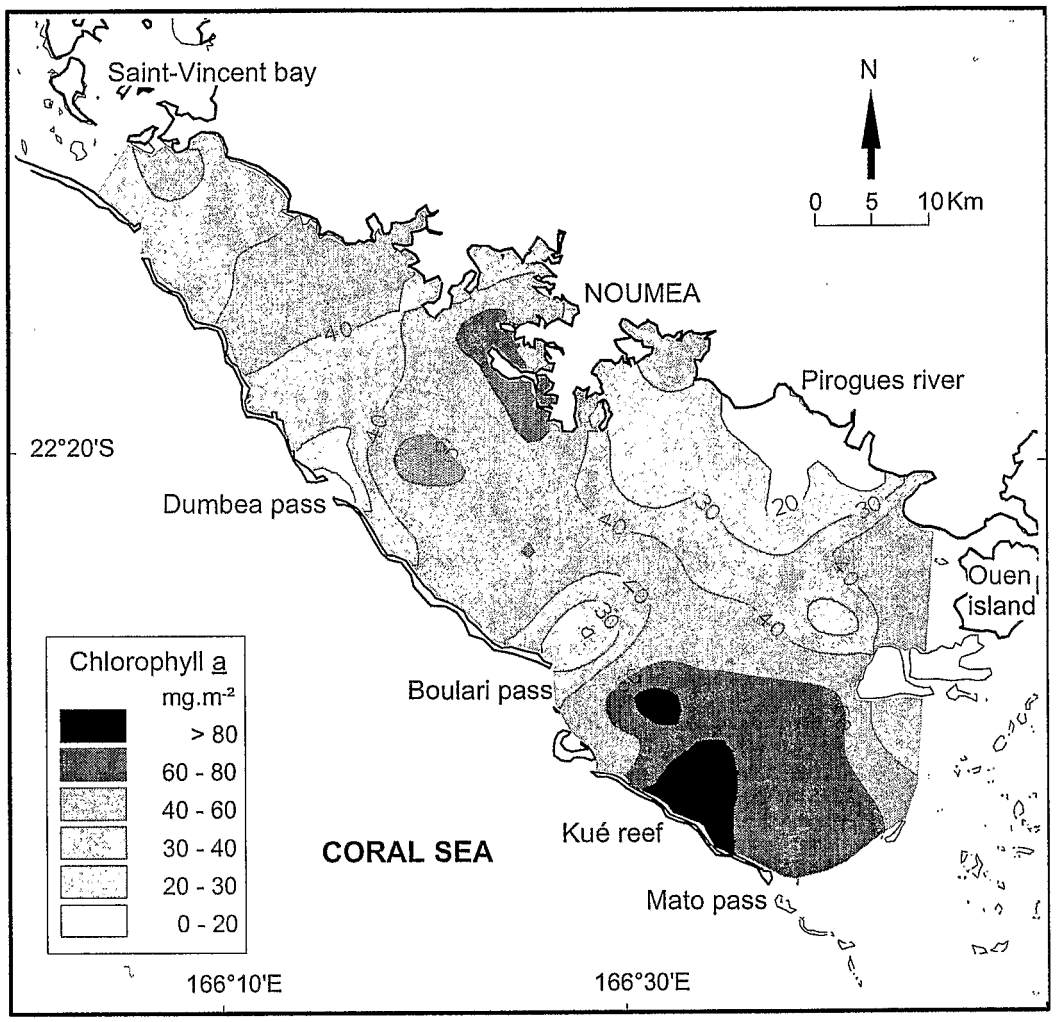


*Figure 2.* Distribution of chlorophyll *a* (top 1 cm) in the south-west lagoon of New Caledonia.

20 mg $m^{-2}$. Chl *a* reaches 60 mg $m^{-2}$ in a small area close to Noumea but the highest quantities of Chl *a*, reaching values in excess of 80 mg $m^{-2}$, were found behind the barrier reef, in the back-reef area of Kué reef. The results of a forward multilinear regression between Chl *a* and the environmental parameters (Table 2) confirmed that Chl *a* increased with distance from shore and decreased with depth and indicated a higher Chl *a* concentration where macrophytes (algae or seagrasses) were present.

The phaeopigment distribution (Figure 3) showed a distinct negative gradient away from shore; the highest values were found in the coastal area, in the bays and at the mouth of the Pirogues River where they reached values in excess of 130 mg $m^{-2}$, while the lowest concentrations occurred near the barrier reef and opposite the passes. The results of a forward multilinear regression between phaeopigments and the environmental parameters show the presence of phaeopigment to be related to the composition of the sediments, with percent mud in the sediment accounting for 43% of the total explained variation (Table 2).

Of the 97 stations with sediments thick enough to be sampled to a depth of 6 cm, the quantities of Chl *a* in each individual layer increased from shore toward the barrier reef. Table 1 shows that the pigment concentrations declined exponentially from the sediment surface towards deeper layers. The upper centimetre of the sediment contained 55% of the total Chl *a* contained in the whole 6 cm thickness. ANOVA revealed a significant variation of Chl *a* and phaeopigment con-

*Table 2.* Coefficients derived from forward stepwise multiple linear regressions between environmental parameters and chlorophyll *a*, and phaeopigments contained in the upper centimeter of sediment (B is a constant, $r^2$ is the cumulative coefficient of determination)

| Variable | B | $r^2$ | Probability | |
|---|---|---|---|---|
| | | | *t* | *p*-level |
| **Chlorophyll *a* (mg m$^{-2}$)** | | | | |
| Intercept | 53.561 | | 10.816 | <0.001 |
| **Depth (m)** | –0.874 | 0.159 | –3.944 | <0.001 |
| **Dist (nm)** | 1.184 | 0.273 | 3.884 | <0.001 |
| **Macrophytes (g Afdw m$^{-2}$)** | 0.197 | 0.333 | 3.156 | <0.002 |
| **Phaeopigments (mg m$^{-2}$)** | | | | |
| Intercept | 40.326 | | 7.684 | <0.001 |
| **%Mud** | 0.706 | 0.437 | 9.967 | <0.001 |
| **Macrophytes (g Afdw.m$^{-2}$)** | 15.211 | 0.541 | 5.074 | <0.001 |

centrations with sediment depth (Chl *a*: $F = 270$ $p < 0.001$; phaeopigments: $F = 206$ $p < 0.001$). *A posteriori* tests showed significant differences between all four layers for Chl *a* but only between three layers for phaeopigments, where the two deepest slices (2–4 cm and 4–6 cm) were not significantly different.

The comparison of sampling dates, using ANOVA, indicated significant temporal differences with time ($F = 5.84$, $p < 0.001$), but an *a posteriori* test failed to identify significantly different groups. Higher Chl *a* concentrations were observed during the spring season than at any other time of the year (Table 3).

## Discussion

### *Spatial and temporal distribution of chloropigments*

The irregular or patchy distribution of pigments (Plante-Cuny, 1978; Van den Hoek et al., 1979) at the small scale is confirmed by the substantial coefficients of variation calculated for the 5 cores collected within the station over a 1 m$^2$ area (Chl *a*: 8–92%; phaeopigments: 4–65%). The differences in CV were not related to environmental parameters, unlike the results noted by Plante-Cuny (1978) who, from 16 cores, had recorded CVs ranging from 11.7 to 77.5% depending on depth and granulometry. Due to the heterogeneity within a station, it is important to take at least 3–5 replicate samples to obtain a representative mean value of the area under study.

The high coefficients of variation among stations (Chl *a*: 60%; phaeopigments: 42%) indicate the variability of pigment concentrations in the lagoon, similar to those observed in the past. For instance Sundbäck (1984) recorded CVs of 41.2% for Chl *a* and 61% for phaeopigments in coastal temperate environments, and Plante et al. (1986) measured CVs of 11 – 29% for Chl *a* over sandy beaches in the Mediterranean.

The decrease in Chl *a* with increasing depth likely reflects the reduced light availability in deeper areas. A similar trend with depth has been reported in the past, such as Sundbäck (1984) for shallow water in temperate environments and Villiers et al. (1987) for tropical environments. The positive correlation observed between Chl *a* and distance from the shore in combination with the negative correlation between mud percentage and distance from shore demonstrates a relationship between mud and the presence of microbenthic Chl *a*. The increase in Chl *a* in the vicinity of macrophytes is most likely linked to an input from epiphytes present on the latter, or to macrophyte debris whose Chl *a* has not yet broken down but it could also be due to the abundance of microalgae. Microalgae seem to be more abundant in the seagrass meadows than on the bare sediment. Moriarty et al. (1985, 1990) found a higher bacterial production on sediment in seagrass communities than on bare sand or on reef flat. As bacteria used a part of the organic nutrients excreted by microalgae (Moriarty et al., 1985) it seems probable that the microalgae are abundant in the vicinity of seagrass. A decrease in Chl *a* biomass near the

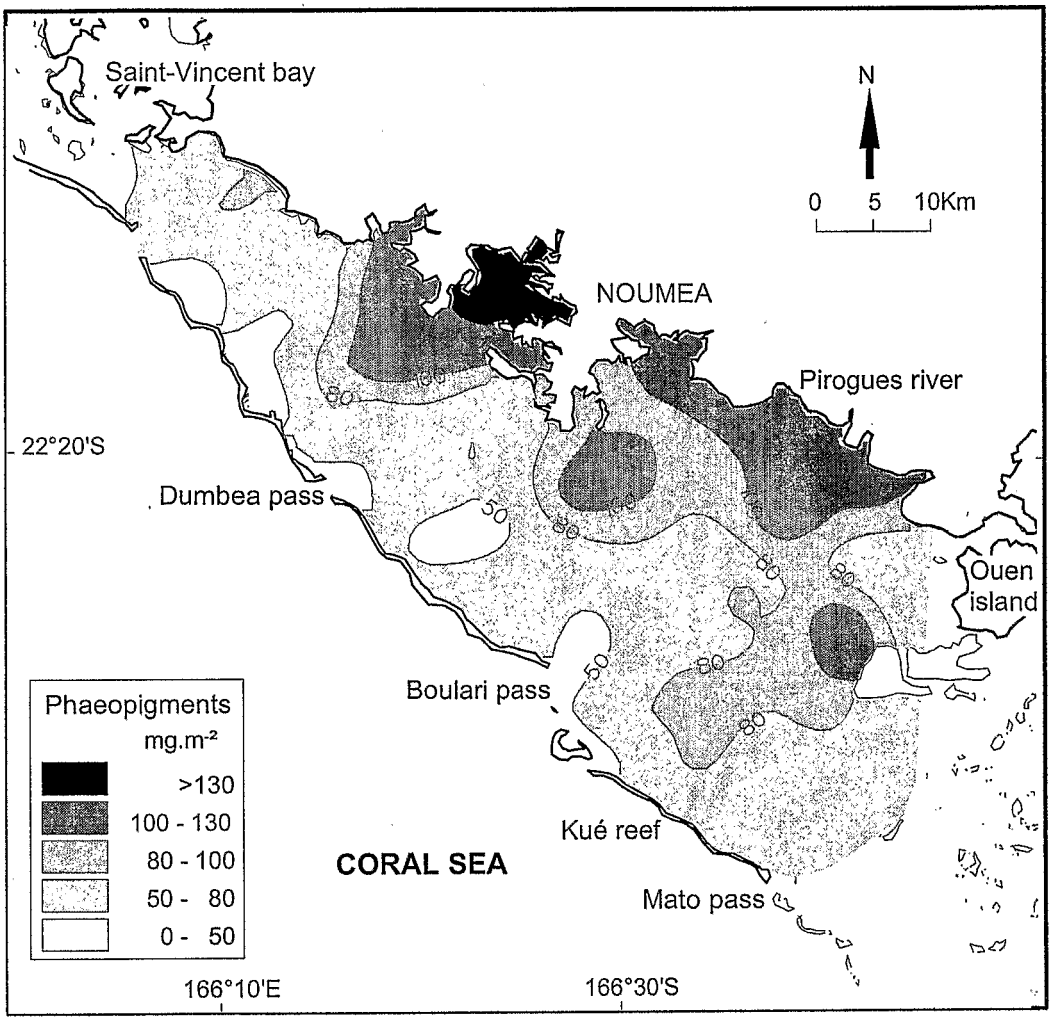


*Figure 3.* Distribution of phaeopigments (top 1 cm) in the south-west lagoon of New Caledonia.

reef passes connecting the lagoon to the open ocean was also observed. This can be related to depth, as there are submarine canyons that correspond to the old rivers in front of the passes. Furthermore, these locations receive oceanic water which has lower nutrients concentrations than the lagoon water (Rougerie, 1986). Low concentrations of Chl *a* in sediments from passes between the lagoon and ocean are also observed in shallow water. Charpy-Roubaud (1986) also showed that in the Tuamotu Islands, the stations poorest in Chl *a* were located at the mouth of the 'hoas' that link the inner lagoon to the open ocean.

The concentration of phaeopigments increased towards the shore, particularly in shallow areas with fine and muddy sediments, similar observations were made in Madagascar (Plante-Cuny, 1978). These find-

*Table 3.* Temporal variation in benthic chlorophyll *a* (mean and standard deviation)

| Months | Chl *a* (mg m$^{-2}$) | SD |
|---|---|---|
| January | 51.5 | 16.6 |
| February | 45.5 | 18.5 |
| April | 37.5 | 18.2 |
| June | 31.1 | 20.8 |
| July | 41.1 | 8.7 |
| August | 32.2 | 10.6 |
| September | 46.1 | 16.0 |
| October | 56.8 | 40.6 |
| November | 75.6 | 23.9 |

*Table 4.* Concentrations of photosynthetic pigments in some tropical areas (Thick: sediment thickness in cm)

| Chlorophyll *a* (mg $m^{-2}$) | Phaeo (mg $m^{-2}$) | Thick (cm) | Depth (m) | Location | Methods used | Authors |
|---|---|---|---|---|---|---|
| 9.6 | 7.2 | | | Tikehau | Acetone 90% | Charpy-Roubaud |
| (2.3–35.7) | (2.2–22.9) | 0–1 | 0.6–40 | (French Polynesia) | Fluorometer | (1986) |
| 17.2 | 17.5 | 0–1 | 0.5–45 | Mururoa | Acetone 90% | Villiers et al. |
| | | | | (French Polynesia) | Lorenzen | (1987) |
| 43.8 | 36.5 | | | Sandy bottoms | | |
| 28.5 | 86.6 | 0–1 | 0–60 | Muddy bottoms | Acetone 90% | Plante-Cuny |
| 38.8 | 49.9 | | | Madagascar | Lorenzen | (1978) |
| 236–907 | 1–31 | 0–3 | 0.5–1 | Takapoto | Acetone 90% | Sournia (1976) |
| 56–140 | 24–29 | 0–3 | 10–17 | (French Polynesia) | Lorenzen | |
| | | | | | Acetone 90% | Bunt et al. (1972) |
| 3.7–22.4 | | 0–1 | Intertidal | Florida | Lorenzen | |
| 47.2 | 78.4 | | | Sw lagoon | Acetone 90% | This study |
| (3–206) | (19–245) | 0–1 | 4–36 | New Caledonia | Lorenzen | |
| 77.0 | 35.0 | | | Ouvea Atoll | Acetone 90% | Clavier & |
| (2–268) | (2–87) | 0–1 | 0–40 | (New Caledonia) | Lorenzen | Garrigue (1993) |

*Table 5.* Distribution of biomasses in the different trophic groups (from Chardy & Clavier, 1988; Garrigue, 1995 and the present study)

| Trophic groups | Biomass (*g AFDW $m^{-2}$ or ** Chl *a* mg $m^{-2}$) | Biomass (gC $m^{-2}$) | Biomass (% of total biomass) |
|---|---|---|---|
| Microphytes | 47.2* | 2.4 | 18.8 |
| Macrophytes | 12.9* | 5.2 | 40.6 |
| **Primary producers** | | **7.6** | **59.4** |
| Suspension feeders | 8.7* | 3.5 | 27.3 |
| Deposit feeders | 3.1* | 1.2 | 9.4 |
| Carnivores | 1.2* | 0.5 | 3.9 |
| **Other trophic groups** | 13.0* | **5.2** | **40.6** |
| Total | | 12.8 | |

ings indicate that these locations are areas of increased deposition, that import and accumulate plant detritus.

The scalar irradiance reaches its maximum in the upper 0–0.5 mm of the sediment (Kuhl et al., 1994; Lassen et al., 1992) so the photic layer of sediments is typically reduced to a few millimetres in thickness (Colijn, 1982; Fenchel & Straarup, 1971; Haardt & Nielsen, 1980). Therefore only the Chl *a* contained in the top sediment layers is photosynthetically active, and thus responsible for primary production. Most of the microbenthic Chl *a* within the south-western lagoon of New Caledonia is found in the superficial sediment layers, 55% within the top centimetre, and 83.5% within the first two centimetres. These results agree with the 75% of the sediment chlorophyll *a* recorded by Cadée & Hegeman (1974) in the top centimetre of intertidal temperate zones. Remarkably, a higher Chl *a* content was measured in the second centimetre than in the first, for a few of the cores, this may reflect the effect of bioturbation on these sites.

Although I was able to demonstrate temporal variations in the quantity of pigments, no significantly different groups of months were statistically recognized. However, Chl *a* concentrations seem to be higher during austral spring. The high coefficients of variation for the monthly average of Chl *a* values (21 – 71%) could indicate a substantial temporal variability, that sometimes exceeds the spatial variability over the entire lagoon (CV: 60%). This could also be a consequence of rapid temporal changes in the study area. These results concur with those of Rizzo & Wetzel (1985), who concluded that the short-term variability in an estuary blurred any seasonal pattern that may underlie this variability. They attributed these results to the rapidity of growth and response time of benthic microflora, along with a small scale spatial heterogeneity. According to some authors, seasonal variations in coastal microphytobenthic biomass in temperate environments have been observed (Shaffer & Onuf, 1983;

Plante-Cuny & Bodoy, 1987; Sundbäck & Jonsson, 1988; Herndl et al., 1989), whereas others found a lack of pronounced seasonal pattern (Cadee & Hegeman, 1974; Colijn & de Jonge, 1984; de Jonge & Colijn, 1994).

*Role of microphytobenthos in the coastal ecosystem*

The mean values for Chl *a* and phaeopigments found in the south-western lagoon of New Caledonia are within the same order of magnitude as those reported for other tropical sandy lagoon bottoms (Table 4). Average Chl *a* values recorded for the two high island lagoons, Madagascar (0–60 m depths) and the south-western lagoon of New Caledonia (0–40 m depths), were similar. However, Chl *a* content in the south-western lagoon was greater than those in Tikehau and Mururoa (two of the French Polynesian atolls), but lower than that of Ouvea Atoll, located north-east of New Caledonia (Clavier & Garrigue, 1993). The maximum Chl *a* values observed for the south-western lagoon are close to those recorded by Sournia (1976) for the atoll of Takapoto (10–17 m depths), but are much lower than those observed by the same author in some foraminifer sands containing symbiontic algae. Some areas of the south-western lagoon contain large amounts of foraminifers (Debenay 1987) such as *Amphisorus hemprichii* Ehrenberg, 1839 (C. Chevillon, pers. comm.), or free corals (up to 345 individuals $m^{-2}$ of *Heteropsammia michelini* Edwards & Haine, 1848 (Chardy et al., 1987)). These organisms are capable of significantly raising the Chl *a* present in these areas, as *Heteropsammia mitchelini* are responsible for 97 – 249 mg $m^{-2}$ of Chl *a* (Garrigue et al., 1992).

The figures used in published work for converting biomass of microalgae to carbon vary widely, from 20 to 120 (De Jonge, 1980; Charpy & Charpy-Roubaud, 1990; for an overview of the subject see Skjoldal, 1982). Assuming a C/chlorophyll *a* of 50 (Charpy & Charpy-Roubaud, 1990), the average biomass of the benthic microflora of the New Caledonian south-western lagoon can be estimated at 2.4 gC $m^{-2}$. This value is within the same order of magnitude as the average values found by de Jonge and Colijn (1994) in temperate regions: 3.2 – 11.0 gC $m^{-2}$ for 0 – 2.0 cm.

The microphytobenthos can be used by the surface deposit feeders that represent about a quarter of the total animal biomass in the overall structure of the lagoon. These animals, that take their food selectively from the water–sediment interface, are especially well represented on the white sand bottom close to the barrier reef (Chardy & Clavier, 1988a) where the microphytobenthos is present in its highest concentration. The dominant species are microphagous gastropods such as *Strombus gibberulus* and *Strombus luhuanus* (Chardy & Clavier, 1988a) that feed on filamentous algae and microalgae on sand grains (Kohn, 1983; Goiran, 1990).

## Conclusion

In the south-western lagoon of New Caledonia, the spatial distribution of the benthic microflora is affected by a combination of several factors: depth – and therefore light level – granulometric characteristics – and therefore the energy environment – and the presence of macrophytes. Microphytobenthic biomass, estimated at 2.4 gC $m^{-2}$, represents half the value of the macrophytobenthic biomass that has been evaluated at 5.2 gC $m^{-2}$ (Garrigue, 1995). These two compartments represents a biomass of 7.6 gC $m^{-2}$ for the primary producers group that would be further increased by taking into account the three others primary producer sub-groups not yet studied: endolithic algae, symbiotic algae and phytoplankton. Compared with other trophic groups evaluated by Chardy & Clavier (1988a), primary producers present the most important biomass in the south-west lagoon of New Caledonia (Table 5).

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