

Photosynthetic pigments of sandy sediments on the north Mediterranean coast: their spatial distribution and its effect on sampling strategies

Raphaël Plante¹, Marie-Reine Plante-Cuny¹ & Jean-Pierre Reys²

¹ Centre d'Océanologie de Marseille, Station Marine d'Endoume, 13007 Marseille, France

² Laboratoire d'Hydrobiologie Marine, Faculté des Sciences de Luminy, 13288 Marseille, Cedex 9, France

ABSTRACT: The distribution of photosynthetic pigment concentrations, as an index of microalgal biomass, was studied on shallow sandy bottoms in the Gulf of Fos near Marseille, France. Analyses of grid and transect samples of surface sediments gave evidence of several patchiness scales, which can be related to the size scales of sedimentary structures: (1) on a large scale (some km), stations located on exposed shores exhibit more heterogeneous distributions than those in sheltered areas; (2) on a medium scale, sand-waves ($\lambda = \text{ca } 10 \text{ m}$) induce accumulation of plant pigments in the depressions; (3) on a small scale, ripple marks ($\lambda = 3 \text{ to } 10 \text{ cm}$) may leave a pigmentary record even after they fade out. The influence of vertical distribution within sediments and of seasonal effects on these horizontal features is analysed. Finally, a sampling strategy is discussed which is based on the maximum dispersal of samples within any previously defined strata. Definition of the strata depends upon the aim of the study.

INTRODUCTION

The contribution to ecosystem primary productivity of those shallow surface sediments which do not harbour a conspicuous macrophytic vegetation was long neglected. It is only during the past 2 decades that interest in these biota has developed. A recent review was given by Colijn & de Jonge (1984). Some studies were devoted particularly to sandy intertidal flats (Grøntved 1962, Steele & Baird 1968, Gargas 1970, Colocoloff & Colocoloff 1973, Plante-Cuny 1973, 1978, Cadée & Hegeman 1974). These workers emphasize the important part played by benthic microphytes in the carbon budget of shallow waters. Consequently, these organisms appear as a prominent link in food webs (Marshall 1970, Sundbäck & Persson 1981, Admiraal et al. 1983, Hudon 1983, Bianchi & Levinton 1984, Montagna 1984). The 'richness' of this ecosystem component is a vague concept which may be expressed statically ('biomass') or dynamically ('production'). Measurements of concentrations of photosynthetic pigments provide an indirect approach to 'potential production' as suggested for example by Margalef (1977) or Colijn & de Jonge (1984).

Spectrophotometric techniques are acknowledged as giving valid figures (Brown et al. 1981), as long as the acidification method is used, for the separate estimation of chlorophyll *a* and pheopigment concentrations in the sediments. As they are easily and quickly employed, they have been widely used since Figueras (1956) (cf. review by Plante-Cuny 1978). Apart from the quality of chemical identification, the reliability of such measurements is largely dependent upon the distribution pattern of microalgae and therefore of pigment values, on and within the sediment. Only a few studies have addressed this aspect of the problem, the first of which was by Odum et al. (1958). Most authors emphasize fluctuations in space or time (Bunt et al. 1972, Riznyk & Phinney 1972, Plante-Cuny 1973, 1977, 1978, Cadée & Hegeman 1974, Estrada et al. 1974, Colijn & Nienhuis 1978, de Heer cited in van den Hoek et al. 1979, Colijn & Dijkema 1981, Riaux 1982, Skjoldal 1982, Shaffer & Onuf 1983, Brotas & Catarino 1984, Colijn & de Jonge 1984, Sundbäck 1984). The aim of the research reported here was to analyse relationships between sedimentary structures and the distribution of pigment values. We considered several spatial scales over a wide sheltered sandy shore.

MATERIAL AND METHODS

Sampling sites. Sand cores were collected in March, June and September 1983 at 2 sites located in the Gulf of Fos 40 km west of the city of Marseille. The first site (sampled only in March) was located on the inner edge of a sand bar, the They de la Gracieuse (Fig. 1a; TG). This area was destroyed by a heavy storm in April 1983 and another site was chosen on the Carteau Beach (CB) in the northwestern part of the Gulf. At both sites, sampling stations were chosen at a selected depth (30 to 60 cm) where dense populations of bivalves are known to occur (*Ruditapes decussatus* and *R. aureus*). Carteau Beach is fairly sheltered from the most frequent winds (N, NW) but exposed to easterly winds. This situation develops 2 types of sedimentary structures (Fig. 1b). These comprise the following: (1) *Sand waves* perpendicular to the shore are built up by lateral transfer currents. These 'dunes' are approximately 5 to 15 m apart and exhibit a few weeks stability. Longitudinal ridges roughly parallel to the shoreline extend deeper than our sampling site. (2) *Ripple*

marks are created by the lapping of waves. While well developed in shallow water they disappear at greater depths. Their wavelength varies between 3 and 10 cm and they exhibit a short time stability: they may disappear within a few hours depending on the prevailing wind changes. Sediments of both sampling sites were well-sorted fine sands. Mean particle diameters were 220 μm and 180 to 200 μm for They and Carteau Beach respectively, and water content was 18 and 19 % respectively. These sites are representative of a large proportion of relatively sheltered sandy shores on the Mediterranean French coast.

Field methods. Coring techniques. Core samples were hand-collected in order to avoid sediment-surface disturbance. After testing 3 different core diameters, corers (plexiglas tubes with rubber stoppers) with internal diameters of 2.6 cm were used in order to study horizontal variations. Larger diameter cores (4.4 cm) were used in the homogenization procedure (see below). The uppermost cm of the sediment core ($\varnothing = 2.6$ cm) was carefully withdrawn by means of an adjustable screw-driven piston and cut off after precise levelling in a 1 cm tall mould ring. This upper centimeter of each core will be considered as the 'sample unit' in further treatments. The same apparatus was used on 2 occasions in order to cut cores into slices down to 20 cm. Sediment samples were immediately placed in the dark at 5°C, and within the same day subsequently frozen at -20°C.

Homogenization procedure; method reliability. The sampling and processing as a whole were tested by using thoroughly hand-mixed surface (0 to 1 cm) sediment collected from 6 randomly distributed large diameter cores ($\varnothing = 4.4$ cm). This sediment was then subsampled in sample units ($\varnothing = 2.6$ cm) and processed in the usual way. Chlorophyll concentrations as well as physical parameters (such as wet weight and water content) showed coefficients of variation which fluctuated around 10 %, a figure which may be considered as satisfactory (Cassie 1962). This procedure was also used when studying the medium-scale distribution.

Sampling design. In order to study different distribution scales, several sampling plans were used. Large-scale variation of heterogeneity was studied at 2 sampling sites located 4 km apart by means of 'grid samples'. Grids had sides 2, 3 or 5 m long and consisted of 15 to 25 'sampling points', each of which included 6 sample units. Medium-scale distribution was investigated by the same grids and by a 5 station transect, 25 m long, along the Carteau Beach aimed at testing the influence of sand-wave profile on microphyte accumulation (stratified sampling on ridges and depressions) (Stations A to E, Fig. 2). Homogenization procedure was used at each of the 5 stations. Small-

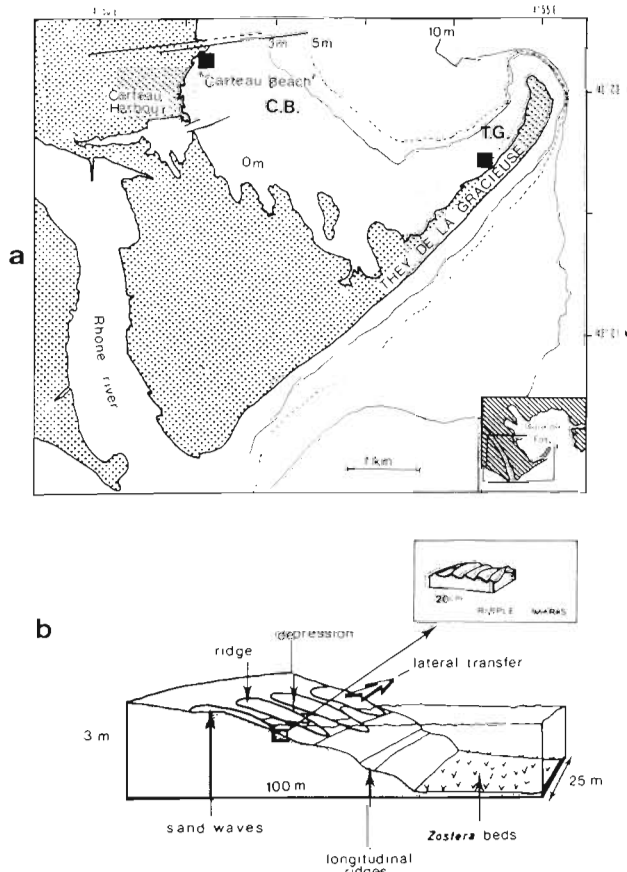


Fig. 1. Sampling sites. (a) General location of the sampling sites. (b) Diagrammatic sketch of sedimentary structures at Carteau Beach

scale distribution was studied by considering the internal variability in the grid samples and by means of transects of 100 contiguous cores along a short distance (3 m) in order to test the influence of ripple marks.

Laboratory methods. After thawing, samples were weighed in the laboratory and plant pigments extracted from the wet sediment sample units with 10 ml of 100 % acetone. Spectrophotometric measurements were made, before and after acidification, according to Lorenzen's formulae (1967) adapted to sediment conditions. The results are expressed as chlorophyll *a* and pheopigment concentrations (Plante-Cuny 1978) either per surface (mg m^{-2}), or dry weight ($\mu\text{g g}^{-1}$), unit. Chlorophyll *a* is considered as 'functional chlorophyll' (Wetzel 1964) corresponding to living phytal material (microphytic cells) whereas pheopigments mainly originate from various detrital plant material or senescent cells.

Statistical treatment. The fluctuations of pigment

concentrations are assumed to be proportional to exponential changes in microphytic cell numbers, which suggests the need for logarithmic transformation of the data (Cassie 1962). Furthermore, these concentrations are continuous variables, thus the coefficient of variation should be used when making comparisons. When employing log-transformed data, this coefficient of variation is expressed as:

$$CV = [\text{antilog}_{10}(s^2/0.4343) - 1]^{1/2} \text{ (Bagenal 1955) (1)}$$

where s^2 = variance of $\log_{10}x$.

The grid samples data were treated by ANOVA which gave estimates of (1) between-sample-units variability and (2) between-sampling-points variability. The contiguous core transects provided data which were submitted to spectral analysis, using a Parzen window ($M = 50$) (Platt & Denman 1975, Laurec 1983).

RESULTS

Influence of gross sedimentary structure: comparison between 2 sites

Comparison between results of grid samples collected on 3 occasions from the 2 sites (TG and CB; Table 1) leads to the following general observations: (1) chlorophyll *a* contents exhibit broader fluctuations at the They de la Gracieuse (TG) station than at Carreau Beach (CB) when considering fluctuations either between individual samples or between sampling points; (2) in general, pheopigment values of the individual samples behave in the same way in both sites, but the variability between sampling points is much higher in the TG site. Average hydrodynamical conditions at the 2 study sites are very different. Sedimentary structures at the CB station remain relatively stable on a monthly time scale: the sand waves were easily recognizable from one sampling date to another. On the other hand, the TG station, which is located on the inner border of a sand-bar, may be invaded by

Table 1. Mean values of the coefficients of variation (CV %) at both sites (TG: They de la Gracieuse; CB: Carreau Beach) from ANOVA operated on pigment values from grid samples expressed as mg m^{-2}

	TG	CB
Chlorophyll <i>a</i>		
between sample units	29.22	15.47
between sampling points	26.78	10.95
Pheopigments		
between sample units	68.74	53.63
between sampling points	87.70	9.44

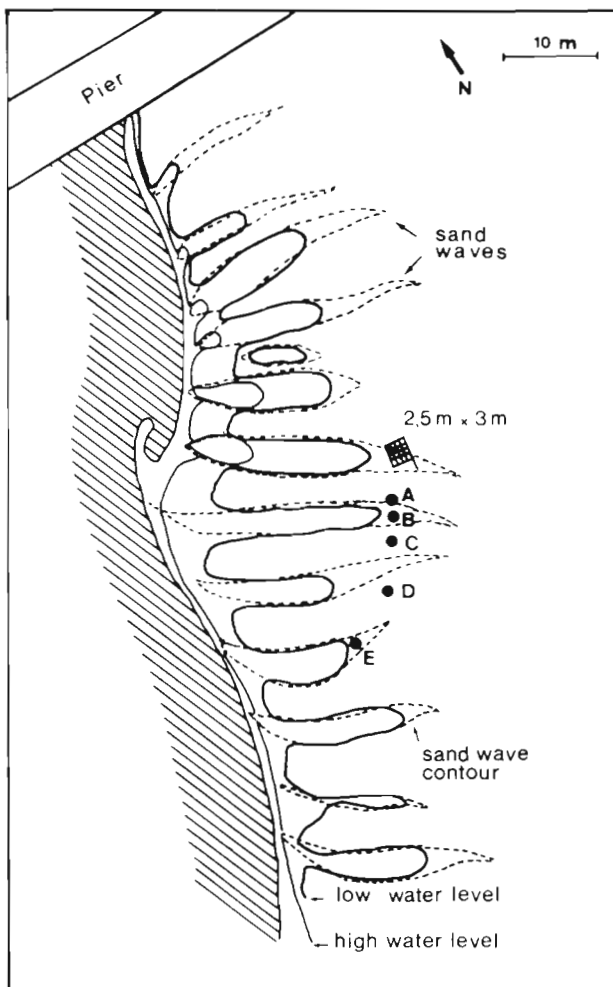


Fig. 2. General situation of the sand wave system on Carreau Beach. Location of the sampling grid and (●) of the stations on ridges and depressions in the 2 Sep 1983 survey

episodic intrusions of sandy or detrital material (dead seagrass leaves). These conditions induce a patchy distribution of plant detritus on the sampling point, which probably explains the marked patchiness observed here at 2 different size scales for the pheopigments (coefficient of variation [CV]: 69 % between sample units and 88 % between sampling points) and, to a lesser extent, for chlorophyll *a* (CV: 29 and 27 %) (Table 1). In the relatively more sheltered area (CB), the living microphytic populations appear to be distributed more evenly (CV: 15 and 11 %).

Influence of medium-scale sedimentary structure within 1 site

The 5 station transect conducted in Carteau Beach (Fig. 2) included 2 stations located on ridges, 2 in depressions and 1 at an intermediate position (Table 2). An ANOVA shows that the station effect is very significant ($p < 0.001$), as is the contrast due to position which demonstrates a clear difference between ridges and depressions ($p < 0.001$) (Table 3). Depressions appear richer than ridges especially for pheopigments which generally correspond to detrital plant material (Table 2). A grid sampling performed in September, located on the slope of a sand wave so that one corner corresponded to a depression axis and the opposite one to a ridge (Fig. 2 & 3b), led to similar conclusions. Both chlorophyll *a* and pheopigments reached obvious maximum values in the depression (Chl *a*: 103 mg m^{-2} ; Pheo: 33 mg m^{-2}) and were relatively low on the ridges (Chl *a*: 60 mg m^{-2} ; Pheo: 15 mg m^{-2}). When considering the transect which crosses a sand dune, this contrast between ridge and depression values appears as a trend (Fig. 4).

Influence of small-scale sedimentary structure

An ANOVA test was carried out on the results from each set of grid samples. These showed that the between-sample-units variation provided a good estimate of the small-scale variability (Table 1). These figures appear higher than the values obtained after the homogenization procedure (ca 10 %). This difference may be explained by the small-scale variability. More precisely, Fig. 4 shows the distribution of pigment concentrations and ripple-mark heights along a 3 m transect (100 cores) across a sand wave. Spectral analysis of ripple-mark data clearly reveals a significant power variation at high frequencies, corresponding to a wavelength of 6.5 cm: this agrees perfectly with the sediment aspect at the sampling time. The spectral shape of pigment data shows no clear power variation at the same frequencies whereas at lower frequencies there are peaks corresponding to a band width of 14 to 19 cm (Fig. 5).

Incidence of vertical distribution

On 2 occasions, vertical pigment profiles were examined by slicing 3 randomly collected cores into 1 cm or 0.33 cm segments. In such shallow waters, chlorophyll *a* is fairly abundant but its vertical distribution is dependent on weather conditions: the June samples (Fig. 6a) were collected on a windy day when the upper 10 cm of sand were mixed up, giving a relatively slow decline of chlorophyll *a* values with depth. Noticeable amounts of chlorophyll *a* were present in the deeper part of the core. On the other hand, in September, conditions were calm before and during sampling. This induced high surface concentrations

Table 2. Mean values of pigment parameters at the Carteau Beach site (5 stations in sand waves; 2 Sep 1983)

	A Intermediate	B Ridge	C Depression	D Depression	E Ridge
Chl <i>a</i> (mg m^{-2})	47.62	33.12	73.99	47.93	55.98
Pheopigments (mg m^{-2})	8.45	8.16	22.21	22.50	16.54

Table 3. ANOVA on pigment concentrations values from the 5 station transect. *** $p < 0.001$

Source of variation	Chlorophyll <i>a</i>			Pheopigments		
	SS	DF	F	SS	DF	F
Between stations	0.38324	4	38.69***	1.15190	4	91.40***
Contrast due to position	0.38122	1	153.96***	0.49023	1	155.72***
Between samples (error)	0.06189	25		0.07869	25	

followed by a steep decrease (Fig. 6b, c). The results suggest that in very calm conditions there are important concentrations of living cells in the immediate

surface layers (0 to 2 cm), whereas degradation products accumulate at slightly greater depths. This situation may prove to be important when calculating the

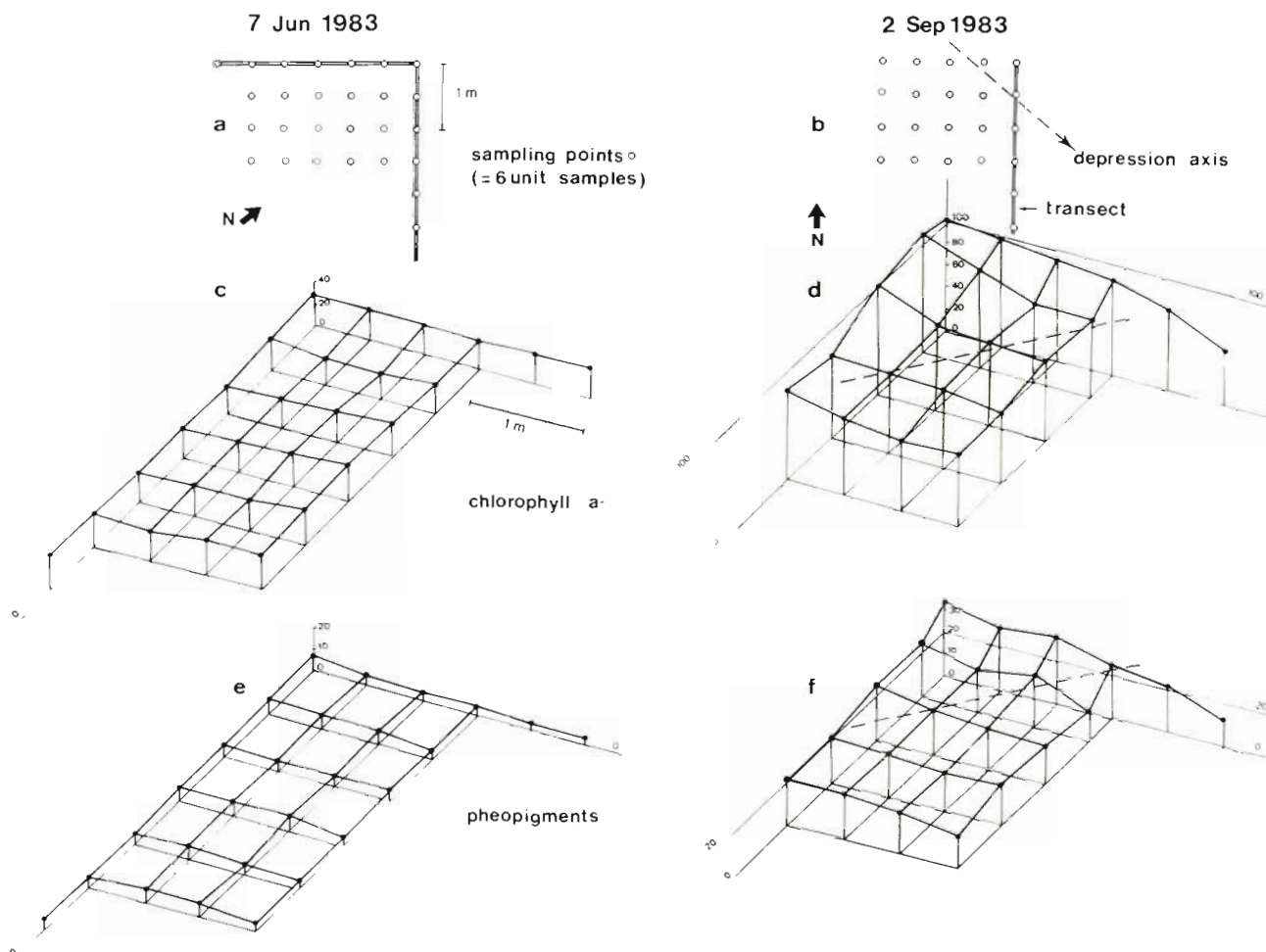
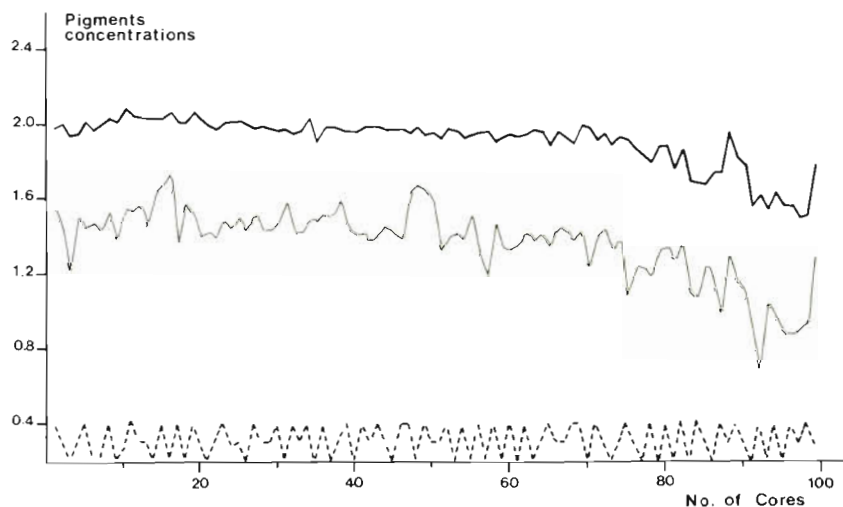


Fig. 3. Diagrammatic sketches of (a, b) sampling plans, (c, d) distribution of chlorophyll a, and (e, f) pheopigment concentrations in grid experiments in Jun and Sep (Carteau Beach). Vertical scales: pigment contents expressed as mg m^{-2} in the upper cm (mean of 6 sample units)

Fig. 4. Pigment concentrations in the upper cm along a 3 m long transect of 100 contiguous cores (Carteau Beach 2 Sep 1983). Thick line: \log_{10} chlorophyll a (mg m^{-2}); light line: \log_{10} pheopigments (mg m^{-2}); broken line: coded height of ripple marks (0 = depression; 0.4 = ridge). The left part of the diagram corresponds to a depression between sand waves (cf. Fig. 3b, d, f)



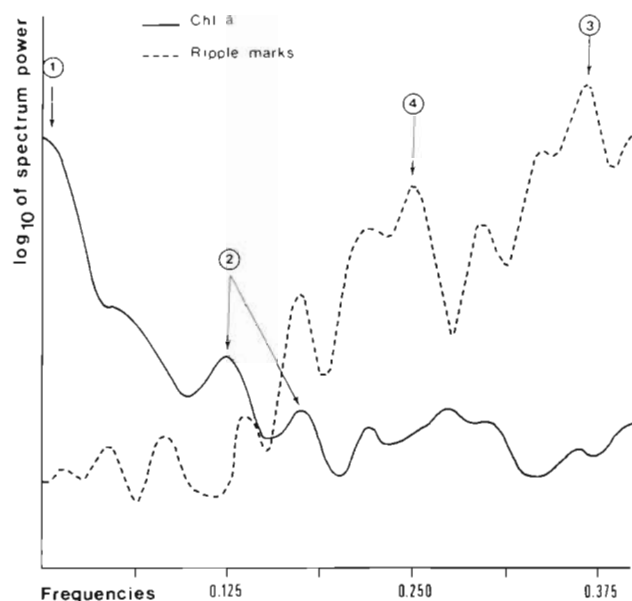


Fig. 5. Spectral analysis of ripple marks and chlorophyll a values from a 100 core transect (cf. Fig. 4). The power spectrum (log values) was recoloured after applying a Parzen's window ($M = 50$). Arrows indicate the main increases of the power spectrum: (1) trend on chlorophyll a values; (2) wavelength of 14 to 19 cm for chlorophyll a; (3) principal wavelength of 6.5 cm for ripple marks; (4) secondary wavelength of 9 cm for ripple marks

amount of functional chlorophyll a per unit area: for instance, in June, the upper cm gave only 37 % of the amount present within the 5 first cm, whereas it represented 78 % in September. The vertical distribution of plant pigments is therefore an important factor to be taken into account when planning a sampling strategy.

Seasonal changes in spatial structure

The grid sampling and homogenization procedures provide comparable figures of pigment concentrations corresponding to different seasons (Table 4). The rela-

tively low chlorophyll a content obtained at the TG station (13.60 mg m^{-2}) is typical of end of winter values. Monthly observations were conducted at this station in 1979, 1980 and 1981 (Bodoy & Plante-Cuny 1980, 1984) and revealed seasonal variations having a maximum in September. The significant difference between pheopigment values obtained from the grid and the values obtained by the homogenization procedure at TG in March is explained by the great patchiness of plant detrital material (and consequently of pheopigment values) at this station. Results from the June and September grid samples at the same site clearly show some seasonal features (Fig. 3): (1) On each occasion chlorophyll a and pheopigment values are distributed in similar patterns. (2) Maximal values are observed at the end of summer. In particular, the storage of detrital material during summer, when production rate is high and weather conditions calm, provides pheopigment values 4 times greater at the end than at the beginning of the summer. At the same time, the heterogeneous distribution of these pheopigment values decreases (CV from 74 to 34 %). (3) The maximal chlorophyll a value does not coincide with maximal heterogeneity: general coefficients of variation calculated with June and September data are not significantly different (CV: 17 and 21 %).

DISCUSSION

At least 3 scales of heterogeneity appear, the dimensions of which correspond to sedimentary features on the beach.

Large-scale heterogeneity

Between the 2 sites, located a few kilometers apart from each other and subject to differing hydrographic conditions, the level of patchiness differs considerably. Although these observations were made at different

Table 4. Mean values of pigment concentrations in the top sediment centimeter, calculated from grid and homogenization data. The variability of a sample, related to a general average, is expressed as a coefficient of variation (between brackets)

	TG		CB
	4 Mar 1983	7 Jun 1983	2 Sep 1983
Chlorophyll a			
$\mu\text{g g}^{-1}$	0.91 (37)	1.82 (15)	4.91 (22)
mg m^{-2}	13.60 (40)	28.08 (17)	75.92 (21)
Homogenization (mg m^{-2})	10.00 (9)	33.65 (10)	79.09 (8)
Pheopigments			
$\mu\text{g g}^{-1}$	0.75 (93)	0.33 (67)	1.25 (30)
mg m^{-2}	7.99 (127)	4.41 (74)	19.48 (34)
Homogenization (mg m^{-2})	0.53 (169)	6.07 (39)	23.03 (8)

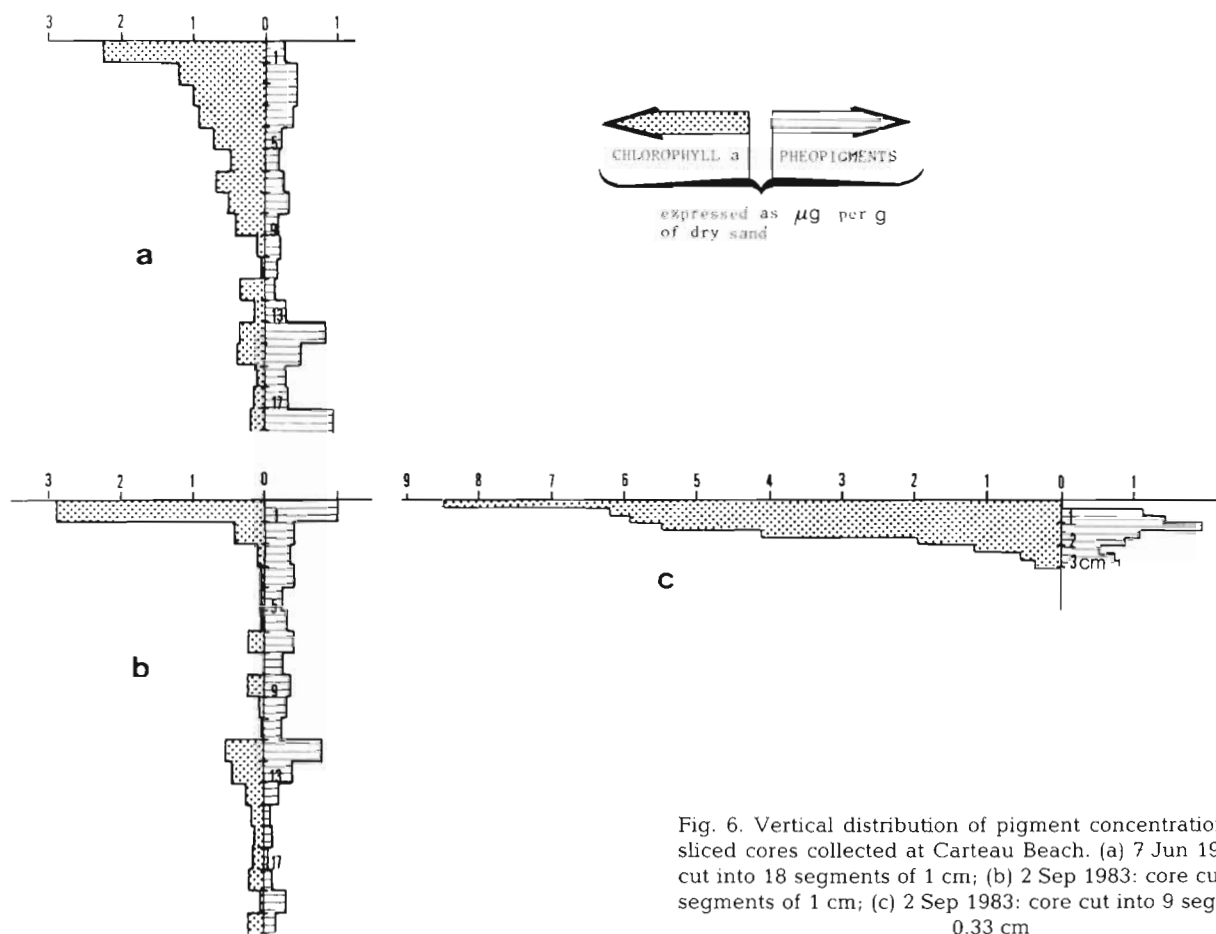


Fig. 6. Vertical distribution of pigment concentrations along sliced cores collected at Carteau Beach. (a) 7 Jun 1983: core cut into 18 segments of 1 cm; (b) 2 Sep 1983: core cut into 20 segments of 1 cm; (c) 2 Sep 1983: core cut into 9 segments of 0.33 cm

seasons, they may be accepted as representative for the whole year, as seasonal fluctuations in microalgal biomass are rather low on the Mediterranean coast of France (Bodoy & Plante-Cuny 1984). Shaffer & Onuf (1983) ranked the 'station' factor among the most important in explaining the overall variation of chlorophyll content in the sediment of a southern California lagoon.

Medium-scale heterogeneity

Within one site on the beach, significant differences appear between the ridges and depressions of sand waves, the wavelength of the latter being ca 10 m. The minimum values of chlorophyll *a* observed on the ridges may be related to increased sand grain mobility and to exposure during occasional low tide conditions which are known to be unfavourable to large diatom species. Under such conditions only minute species remain attached to sand grains (Round 1979). Thus it is probable that sand-dwelling microphytes respond to such medium-scale variation in sedimentary conditions, in much the same way as do meiofauna (cf. McLachlan & Hesp 1984).

Small-scale heterogeneity

Within one station variability was observed at 2 distinct levels: (1) average chlorophyll *a* values obtained from each sampling point are distributed rather evenly over the grid; (2) a conspicuous patchiness exists between sample units at these sampling points. The co-occurrence of these 2 levels may explain the consistent patchiness in small-scale observations recorded by some authors (Odum et al. 1958, Bunt et al. 1972, Plante-Cuny 1978, De Heer cited in Hoek et al. 1979, Riaux 1982). Others, such as Sundbäck (1984), observed low variation in similar data, e.g. CV = 12 or 13 % for shallow sands of the Baltic Sea, which is close to the 10 % value that we obtained after the homogenization procedure. The same observations can be made about pheopigment values, even though their CV remains much higher at all levels. The smaller scale of detectable variability is of the same order of magnitude as our core diameters but no evidence could be found for any relation with the wavelength of ripple marks, probably because of the rapid ripple shifting under normal wave conditions. This result agrees with those of Skjoldal (1982) obtained from similarly mixed

sediments. Jenness & Duineveld (1985) also give evidence of the shifting of sand ripples resulting in the burial of pigments, even in deep water. Moreover, the residual effect of previous events may be influencing the results as we find a 14 to 19 cm wavelength in the spectral analysis which probably originates from larger ripple marks left by earlier transitory bad weather conditions, which persisted long enough to allow the settlement of microphytic cells in the depression. Hogue & Miller (1981) have suggested that patchy accumulations of plant material may persist even when the ripple mark profile is erased.

Sampling strategy

When designing a sampling strategy for studies on benthic phytal biomass temporal variations must, of course, be given primary consideration. Thus factors such as light or temperature, and edaphic factors (hydrodynamism and sediment mobility) fluctuate seasonally. However, in any study of plant biomass per surface unit, it should be kept in mind that when sand-mixing conditions prevail, the upper cm may contain only a part of the total pigment content. As stated by Marshall et al. (1971), if chlorophyll *a* values are to be considered a useful index of probable microbenthic primary production (or of the food available for deposit feeders for instance), the representativeness of surface sediment samples should only be accepted if this has been demonstrated by an appropriate sampling programme. In any study in sandy areas similar to those described here, such a sampling programme should take into account variation in the scale of topographic features. The present study suggests that the most important levels of variation are found (1) between sites (km scale), (2) between stations (m scale), (3) between sample units (cm scale), whereas the between-sampling-points variation (dm scale) appears less important. Consequently, if one is interested in the average value from a given site at a given season, sampling effort should be distributed over many stations and include a few sampling units per station. For example, in the conditions of our study, we found that 40 stations (with 1 sample unit of homogenized sediment per station) were required to reach a precision level of the mean of $\pm 10\%$ at a significance level (α) of 5%.

Acknowledgements. Some aspects of this work were supported by CNRS (ATP No. 98265). We thank Drs. S. Frontier, A. Sournia, H. R. Skjoldal and 2 anonymous reviewers for their constructive criticism of the manuscript and Dr. T. H. Pearson for revising the English version.

LITERATURE CITED

- Admiraal, W., Bouwman, L. A., Hoekstra, L., Romeyn, K. (1983). Qualitative and quantitative interactions between microphytobenthos and herbivorous meiofauna on a brackish intertidal mud flat. *Int. Revue ges. Hydrobiol.* 68: 175-191
- Bagenal, M. (1955). A note on the relation of certain parameters following a logarithmic transformation. *J. mar. biol. Ass. U.K.* 34: 289-296
- Bianchi, T. S., Levinton, J. S. (1984). The importance of microalgae, bacteria and particulate organic matter in the somatic growth of *Hydrobia totteni*. *J. mar. Res.* 42: 431-443
- Bodoy, A., Plante-Cuny, M. R. (1980). Evaluation simultanée des biomasses et productions primaires phytoplanctonique et microphytobenthique en milieu côtier. *C. r. hebd. Séanc. Acad. Sci., Paris* 290: 667-670
- Bodoy, A., Plante-Cuny, M. R. (1984). Relations entre l'évolution saisonnière des populations de palourdes (*Ruditapes decussatus*) et celle des microphytes benthiques et planctoniques (Golfe de Fos, France). *Haliotis* 14: 71-78
- Brotas, V., Catarino, F. (1984). Microfitobentos do estuário do Tejo. *Act. 4º Simposio Iberico Estudos do Benthos Marinho, Lisboa* 3: 119-129
- Brown, L. M., Hargrave, B. T., Mac Kinnon, M. D. (1981). Analysis of chlorophyll *a* in sediments by high-pressure liquid chromatography. *Can. J. Fish. Aquat. Sci.* 38: 205-214
- Bunt, J. S., Lee, C. C., Lee, E. (1972). Primary productivity and related data from tropical and subtropical marine sediments. *Mar. Biol.* 16: 28-36
- Cadée, G. C., Hegeman, J. (1974). Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.* 8: 260-291
- Cassie, R. M. (1962). Microdistribution and other error components of ^{14}C primary production estimates. *Limnol. Oceanogr.* 7: 121-130
- Colijn, F., de Jonge, V. N. (1984). Primary production of microphytobenthos in the Ems-Dollard Estuary. *Mar. Ecol. Prog. Ser.* 14: 185-196
- Colijn, F., Dijkema, K. S. (1981). Species composition of benthic diatoms and distribution of chlorophyll *a* on an intertidal flat in the Dutch Wadden Sea. *Mar. Ecol. Prog. Ser.* 4: 9-21
- Colijn, F., Nienhuis, H. (1978). The intertidal microphytobenthos of the 'Hohe Weg' shallows in the German Wadden Sea. *Forschungsstelle Insel Küstenschutz Norderey Jahresbericht* 29: 149-174
- Colocoloff, M., Colocoloff, C. (1973). Recherches sur la production primaire d'un fond sableux. 2. Méthodes. *Tethys* 4: 779-800
- Estrada, M., Valiela, I., Teal, J. M. (1974). Concentration and distribution of chlorophyll in fertilized plots in a Massachusetts salt marsh. *J. exp. mar. Biol. Ecol.* 14: 47-56
- Figueras, A. (1956). Moluscos de las playas de la Ria de Vigo. I. Ecología y distribución. *Investigación pesq.* 5: 51-87
- Gargas, E. (1970). Measurements of primary production, dark fixation and vertical distribution of the microbenthic algae in the Øresund. *Ophelia* 8: 231-253
- Grøntved, J. (1962). Preliminary report on the productivity of microbenthos and phytoplankton in the Danish Wadden Sea. *Meddr Kommn Danm. Fisk.-og Havunders., N.S.* 3: 347-378
- Hoek, C., van den, Admiraal, W., Colijn, F., de Jonge, V. N. (1979). The role of algae and seagrasses in the ecosystem

- of the Wadden Sea: A review 'The microphytobenthos: the benthic diatoms and bluegreens inhabiting the sand and mud flats'. In: Wolff, W. J. (ed.) Flora and vegetation of the Wadden Sea. Report 3 of the Wadden Sea Working Group, Texel, p. 9–206
- Hogue, E. W., Miller, C. B. (1981). Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *J. exp. mar. Biol. Ecol.* 53: 181–191
- Hudon, C. (1983). Selection of unicellular algae by the littoral amphipods *Gammarus oceanicus* and *Calliopius laeviusculus* (Crustacea). *Mar. Biol.* 78: 59–67
- Jenness, M. I., Duineveld, G. C. A. (1985). Effects of tidal currents on chlorophyll *a* content of sandy sediments in the southern North Sea. *Mar. Ecol. Prog. Ser.* 21: 283–287
- Laurec, A. (1983). Traitement des signaux quantitatifs et implications dans l'échantillonnage. In: Frontier, S. (ed.) Stratégies d'échantillonnage en écologie. Masson, Paris, p. 217–270
- Lorenzen, C. J. (1967). Determination of chlorophyll and pheo-pigments: spectrophotometric equations. *Limnol. Oceanogr.* 12: 343–346
- Margalef, R. (1977). *Ecologia*. Omega, Barcelona
- Marshall, N. (1970). Food transfer through the lower trophic of the benthic environment. In: Steele, J. H. (ed.) Marine food chains. Oliver and Boyd, Edinburgh, p. 52–66
- Marshall, N., Oviatt, C. A., Skauen, D. M. (1971). Productivity of the benthic microflora of shoal estuarine environments in Southern New England. *Int. Revue ges. Hydrobiol.* 56: 947–956
- McLachlan, A., Hesp, P. (1984). Faunal response to morphology and water circulation of a sandy beach with cusps. *Mar. Ecol. Prog. Ser.* 19: 133–144
- Montagna, P. A. (1984). *In situ* measurement of meiobenthic grazing rates on sediment bacteria and edaphic diatoms. *Mar. Ecol. Prog. Ser.* 18: 119–130
- Odum, H. T., McConnell, W., Abbott, W. (1958). The chlorophyll *a* of communities. *Publ. Inst. mar. Sci. Univ. Texas* 5: 65–96
- Plante-Cuny, M. R. (1973). Recherches sur la production primaire benthique en milieu marin tropical. 1. Variations de la production primaire et des teneurs en pigments photosynthétiques sur quelques fonds sableux. Valeur des résultats obtenus par la méthode du ¹⁴C. *Cah. O.R.S.T.O.M. ser. Océanogr.* 11: 317–348
- Plante-Cuny, M. R. (1977). Pigments photosynthétiques et production primaire du microphytobenthos d'une lagune tropicale, la lagune Ebrié (Abidjan, Côte d'Ivoire). *Cah. O.R.S.T.O.M., ser. Océanogr.* 15: 3–25
- Plante-Cuny, M. R. (1978). Pigments photosynthétiques et production primaire des fonds meubles néritiques d'une région tropicale (Nosy-Bé, Madagascar). *Trav. Doc. O.R.S.T.O.M.* 96: 1–359
- Platt, T., Denman, K. L. (1975). Spectral analysis in ecology. *Ann. Rev. Ecol. Syst.* 6: 189–210
- Riaux, C. (1982). La chlorophylle *a* dans un sédiment estuarien de Bretagne Nord. *Annls Inst. océanogr.*, Paris 58: 187–205
- Riznyk, R. Z., Phinney, H. K. (1972). The distribution of intertidal phytoplankton in an Oregon estuary. *Mar. Biol.* 13: 318–324
- Round, F. (1979). A diatom assemblage living below the surface of intertidal sand flats. *Mar. Biol.* 54: 219–223
- Shaffer, G. P., Onuf, C. P. (1983). An analysis of factors influencing the primary production of the benthic microflora in a southern California lagoon. *Neth. J. Sea Res.* 17: 126–144
- Skjoldal, H. R. (1982). Vertical and small-scale horizontal distribution of chlorophyll *a* and ATP in subtropical beach sand. *Sarsia* 67: 79–83
- Steele, J. H., Baird, I. E. (1968). Production ecology of a sandy beach. *Limnol. Oceanogr.* 13: 14–25
- Sundbäck, K. (1984). Distribution of microbenthic chlorophyll *a* and diatom species related to sediment characteristics. *Ophelia, Suppl.* 3: 229–246
- Sundbäck, K., Persson, L. E. (1981). The effect of microbenthic grazing by an amphipod *Bathyporeia pilosa*, Lindström. *Kieler Meeresforsch.* 5: 573–575
- Wetzel, R. G. (1964). A comparative study of the primary productivity of higher aquatic plants, periphyton and phytoplankton in a large shallow lake. *Int. Revue ges. Hydrobiol.* 49: 1–61