



Journal of Experimental Marine Biology and Ecology 316 (2005) 231–241

**Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY**

www.elsevier.com/locate/jembe

Benthic response to ammonium pulses in a tropical lagoon: implications for coastal environmental processes

Jacques Clavier^{a,*}, Guy Boucher^b, Laurent Chauvaud^a,
Renaud Fichez^c, Sandrine Chifflet^d

^aUMR CNRS 6539, IUEM, Place Copernic, 29280 Plouzané, France

^bUMR CNRS 5178 BOME, DMPA MNHN, 61 rue Buffon, 75005 Paris, France

^cIRD, Centre d'Océanologie de Marseille, Station Marine d'Endoume, Rue de la Batterie des Lions, 13007 Marseille, France

^dCentre IRD, BP A5, Nouméa, New Caledonia

Received 23 June 2004; received in revised form 1 October 2004; accepted 2 November 2004

Abstract

In New Caledonia, the benthic communities living in the coral reef lagoon around Noumea city are subjected to regular shifts from oligotrophic conditions typical of lagoon waters to nutrient enrichment due to waste water inputs. The influence of ammonium pulses on microphytobenthos production was experimentally tested under varying light intensities in the vicinity of Noumea. Benthic oxygen, ammonium and silicon fluxes at the sediment–water interface were measured in situ using benthic enclosures. Three ammonium concentrations were tested. Gross primary production was doubled with a 13.8 $\mu\text{mol l}^{-1}$ ammonium concentration increase. Fitted PI curves showed that maximum production (F_{max}) was linearly related to ammonium concentration, but not the optimal irradiance (I_k). Silicon fluxes were characterized by dissolution in the absence of light, a process that declined with increasing illumination. These results were attributed to microphytobenthos activity, mainly diatoms that are nutrient-limited and strongly reactive to ammonium inputs. Production may result from a multiplication of cells, but migration up to the water sediment interface may also be involved. Oxygen consumption was also significantly influenced by ammonium concentration as a positive linear relationship with added ammonium concentration was established. Even during short-term experiments, ammonium enrichment stimulated photoautotrophic production, increasing the energy available to heterotrophs. Furthermore, microbenthic activities as well as nitrate production were increased by ammonia-oxidizing bacteria able to grow chemolithotrophically at the expense of oxygen. Therefore, in the study area, pulses of urban waste waters resulted in a decrease of plant-related autotrophy in benthic communities.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Eutrophication; Metabolism; Microphytobenthos; Nutrient; Tropical lagoon

* Corresponding author. UMR 6539, Institut Universitaire Européen de la Mer, Technopole Brest-Iroise, Place Nicolas Copernic, F-29289 Plouzané, France. Tel.: +33 298 498 785; fax: +33 298 498 645.

E-mail address: Jacques.Clavier@univ-brest.fr (J. Clavier).

1. Introduction

Discharge of nutrients from nearby urban areas is becoming a major source of eutrophication in coastal waters (Valiela et al., 1992; Bowen and Valiela, 2001). The problem is particularly acute in tropical countries (Hatcher et al., 1989) where, for economical reasons, most of the cities have limited facilities to prevent pollution, and urban waste waters are often discharged directly to waterways or to the sea (Pastorok and Bilyard, 1985; Grigg, 1994). Hence, the marine environment around sewer outlets is subject to nutrient input whose intensity and frequency are governed by the conjunction of the effects of tide, wind and magnitude of the outflow. In coral reef environments, the sheltered lagoon further retain urban waste waters and the impact of polluted water will differ according to lagoon size and water residence time (Naim, 1993). The whole system can be affected by eutrophication, including the reef itself (Hatcher et al., 1989; Johnstone et al., 1989). Although in large lagoons, such as the New Caledonia lagoon, the impact may be constrained to coastal waters this often includes valuable sites in terms of recreational and tourism activity (Labrosse et al., 2000).

In New Caledonia, the city of Noumea has a population of around 100,000 inhabitants and essentially extends over a 10-km long peninsula. Numerous urban waste water sources flow to the SW lagoon (2000 km²) through a diffuse network. Sewage waters are progressively diluted in oligotrophic lagoon water (Bujan et al., 2000) as a combined function of geomorphology, tidal conditions and wind forcing (Douillet, 1998; Douillet et al., 2001). Benthic communities around Noumea are, therefore, subjected to regular shifts from oligotrophic to nutrient enriched conditions.

Increases in nutrient inputs generally affect the structure and the function of biological systems (Cloern, 2001). Sedentary benthic organisms have to adapt their life strategies to the characteristics of the environment they are living in (Grall and Chauvaud, 2002). Primary producers are generally the first to be affected and proliferation of macrophyte in nutrient enriched areas are now well documented (Duarte, 1995; de Casabianca et al., 1997; Kuffner and Paul, 2001; Bokn et al., 2003;

Fong et al., 2004; Invers et al., 2004), although contradictory results were obtained in the ENCORE experiment (Koop et al., 2001). Previous studies have shown that ammonium is a limiting factor of seagrass bed production in the SW lagoon of New Caledonia (Boucher et al., 1994). These in situ experiments have, however, been conducted at constant irradiance or in dark, conditions that did not allow for the calculation of daily production. The response of the microphytobenthos to nutrient increase has rarely been studied (Dizon and Yap, 1999; Miyajima et al., 2001; Dizon and Yap, 2003; Tyler et al., 2003), especially under natural conditions. Benthic microalgal production has been studied extensively in intertidal and estuarine habitats. Nutrients concentrations do not generally control microphytobenthic production (Paterson et al., 1986; Sundbäck and Jönsson, 1988; Kromkamp et al., 1995) since other environmental parameters (light, sediment parameters, space availability) are much more limiting factor (Collos, 1987; Rizzo, 1990; Irigoien and Castel, 1997). However, benthic primary production reduces nitrate benthic fluxes by 20% (Graneli and Sundbaeck, 1985; Rizzo, 1990) and a positive relationship between benthic microalgae biomass and increased nutrient loading has been established (de Jonge, 1990; Philippart and Cadée, 2000).

This paper presents experimental testing of the influence of ammonium pulses on microphytobenthos production and community respiration on sandy bottoms at different light intensities in the vicinity of Noumea sewage outlets. The main question addressed was to determine if short-term inputs could significantly affect benthic primary production and thus increase available energy for benthic communities.

2. Materials and methods

2.1. Study site

In situ experiments were conducted for 6 days at the end of August 2001 during the cool season. The study site (22°18.43' E–166°26.80' S) was located near a fringing reef and no more than 200 m away from the shore at a depth of 1.5–2.5 m depending on

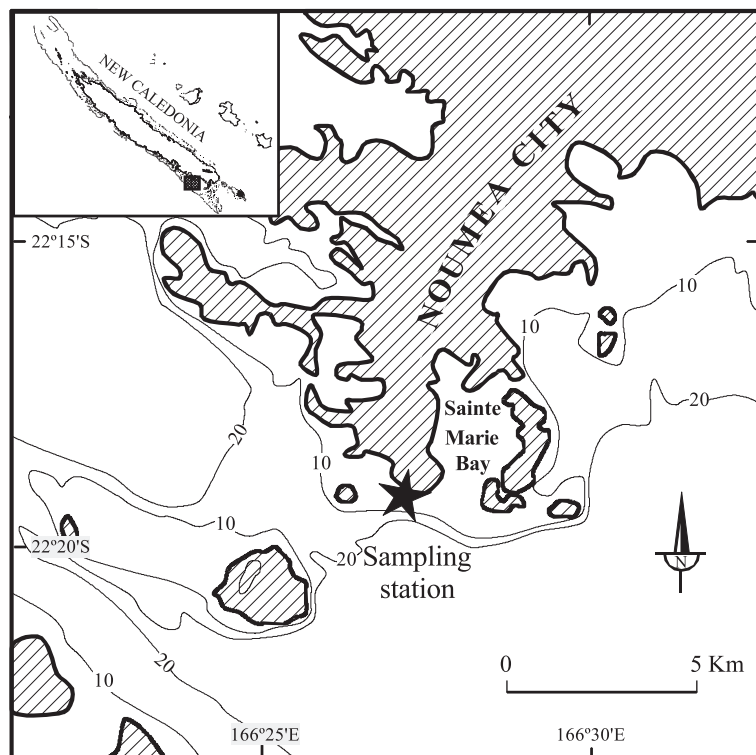


Fig. 1. Location of the sampling site in the New Caledonia lagoon.

the tide (Fig. 1). Sediments were devoid of macrophytes and primary production was exclusively performed by the microphytobenthos. The sediment surface was smooth without noticeable effects of bioturbation. Our experimental site corresponds with the grey sand community using the classification scheme of Chardy et al. (1988).

2.2. Incubation procedure

Benthic fluxes at the water–sediment interface were estimated in situ using flux chambers already operating in the lagoon (Boucher and Clavier, 1990; Boucher et al., 1994, 1998; Clavier et al., 1994, Clavier and Garrigue, 1999). Three clear acrylic hemispheres were fastened on 0.2-m² PVC cores pushed ca. 10 cm into the substrate by SCUBA divers, ensuring a minimum of sediment disturbance. Enclosed water (about 55 l) was homogenised with adjustable submersible pumps (2 l mn⁻¹).

For each incubation run, three ammonium concentrations were tested: (i) natural conditions in

enclosure 1 considered as a control, (ii) injection of 100 ml of a 2500 $\mu\text{mol l}^{-1}$ ammonium chloride solution in enclosure 2 and (iii) injection of 100 ml of a 7500 $\mu\text{mol l}^{-1}$ ammonium chloride solution in enclosure 3. Resulting concentrations of ca. 5 and 15 $\mu\text{mol l}^{-1}$ were finally obtained in enclosures 2 and 3, respectively. A recent fluorimetric detection technique adapted to low ammonium concentrations (K erouel and Aminot, 1997) has been applied to New Caledonia lagoon water (Chifflet et al., 2003) yielding NH_4 concentrations mostly in the range 0.3–0.8 $\mu\text{mol l}^{-1}$ in the coastal zone. Experimental enrichment levels were kept moderate. Values were mostly lower than those measured in the interstitial waters of lagoon sediments (ca. 25 $\mu\text{mol l}^{-1}$, Boucher et al., 1994). No noticeable wall effects of ammonium uptake have been demonstrated in this type of in situ incubation chamber (Boucher et al., 1994).

To mimic ammonium pulses, a series of incubations were carried out for 1.5 h, replicated up to four times a day at different light intensities, including

night incubations after sunset. A total of 19 measurement series were obtained for each ammonium concentration. The enclosures were opened for 30 min between successive incubations to restore ambient conditions. PVC bases were left at the same place during the whole experiment but were cleaned every day to avoid fouling growth. Oxygen, ammonium and silicate fluxes were measured.

The oxygen concentration (mg l^{-1}) in each enclosure was measured in situ using polarographic probes connected to a three-way oxygen logger respirometer set in a waterproof container. Additionally, a LICOR quantum sensor (LI-192SA) was deployed inside one of the hemispheres to record the actual amount of photosynthetically active radiation (PAR, 400–700 nm; $\mu\text{mol m}^{-2} \text{s}^{-1}$) available for the enclosed photosynthetic organisms. Oxygen and light intensity were recorded in situ every 5 s on a numeric data logger. Replicate seawater samples were collected by SCUBA divers using 100-ml plastic syringes, at the beginning and end of incubations, to measure ammonium concentrations. As lagoon microphytobenthic production is known to be mainly due to diatoms (Uthicke and Klumpp, 1997, 1998; Uthicke, 2001), silicate was also measured and silica fluxes assessed. All of these incubations were carried out at ambient light.

Sediment samples were collected at random outside the enclosures at the beginning of the study with 5.3 cm^2 cores to determine sediment size structure (three samples) and pigment content in the top centimetre of sediment (six replicates). Sediment sampled for pigment content were lyophilised and stored in the dark.

2.3. Sample processing

The recorded light intensity and oxygen values were averaged every minute. An in situ 24-h average irradiance profile was calculated for the study period using all collected data. Net hourly photosynthetic production was calculated as the difference between oxygen concentration at the beginning and at the end of incubations, after checking over the regularity of continuously recorded data. Oxygen data were transformed to CO_2 fluxes using community photosynthetic (gross O_2 production rate/gross CO_2 consumption rate=1.03) and respiratory (CO_2 produc-

tion rate/ O_2 consumption rate=1.14) quotients previously established for the New Caledonia lagoon (Clavier et al., 1994).

Ammonium samples were preserved for less than half an hour after collection and stored in a cool dark place before addition of reagents and analysed according to the ortho-phthalaldehyde method (K  rouel and Aminot, 1997; Chifflet et al., 2003). Samples for silicate analysis were stored in a dry cool place until analysed with a Technicon autoanalyser (Fanning and Pilson, 1973).

Sediment organic content was calculated by measuring the loss of sediment dry weight after ignition at 450 °C. Pigments were extracted using 90% acetone for 24 h. After filtration of the extract, optical densities were assessed on a spectrophotometer at 750 and 665 nm before and after acidification by 0.5 N HCl (Garrigue and DiMatteo, 1991). Lorenzen (1967) equations were used to calculate functional chlorophyll *a* concentration (mg m^{-2}).

2.4. Sewage waters

To determine the order of magnitude of Noumea sewage water nutrient concentrations, samples were taken from the outlet of a drain, in Sainte Marie Bay, near the study area (Fig. 1). Water samples were collected by hand every hour from 7 to 18 h. Ammonium, nitrates+nitrites, phosphate and silicate concentration were determined using above methods.

2.5. Data treatment

Net production in oxygen, ammonium and silicate fluxes ($\text{mmol m}^{-2} \text{h}^{-1}$) were plotted as a function of in situ light intensity. An exponential function (Gattuso et al., 1996; Boucher et al., 1998; Clavier and Garrigue, 1999) was fitted to the community productivity:

$$F = F_{\text{max}}(1 - \exp(-I/I_k)) + r$$

where: F =net oxygen, ammonium or silicate flux; F_{max} =rate of maximal flux; I =irradiance; I_k =optimum irradiance with $F_g=F_{\text{max}}$; and r =flux during the night. Model adjustment was performed using the mean square method with Marquardt's algorithm.

Model parameters and irradiance values were used to calculate oxygen, ammonium and silicate fluxes

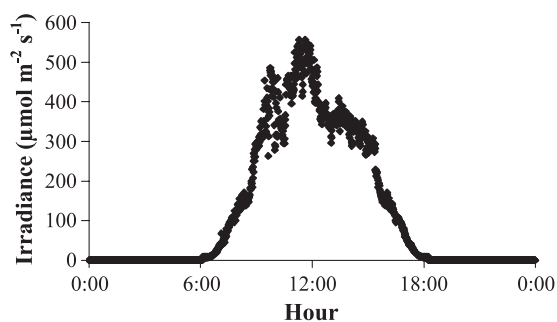


Fig. 2. Daily evolution of average light intensity during the experiments.

every minute over a 24-h period. Net daily oxygen flux (P_n , $\text{mmol m}^{-2} \text{day}^{-1}$) is the sum of the 1440 values per minute. Gross daily community production (P_g , $\text{mmol m}^{-2} \text{day}^{-1}$) is P_n plus the daily respiration (R). Respiration was measured during night incubations and assumed to be constant over a 24-h period. Similarly, ammonium and silicate benthic uptakes were calculated as the sum of the net flux at light and the flux at night per minute.

3. Results

3.1. Environmental parameters

A sediment layer 10 cm thick with a mean particle size of 0.53 (ϕ scale, corresponding to medium sand, Wentworth, 1922) covered a limestone hard ground. The mud fraction ($<63 \mu\text{m}$) accounted for only 4.6% of the sediment and the mean organic matter content was 3.3%. The mean chlorophyll *a* and phaeopigment concentrations in the top centimetre of sediment were 59.06 mg m^{-2} (S.E. 10.84) and 63.26 mg m^{-2} (S.E. 7.07), respectively. The sea water temperature during the experiments was $22.0 \text{ }^\circ\text{C}$. During the study, the sun rose approximately at 6 h and set at 18 h. Underwater

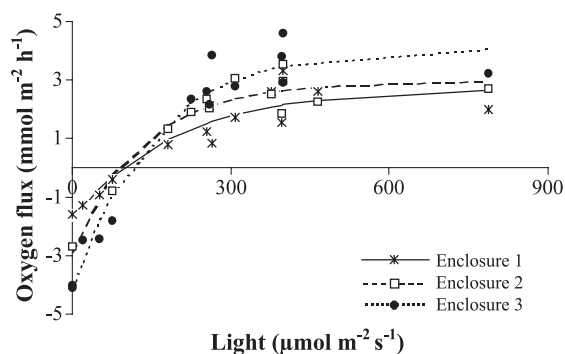


Fig. 3. Fitted P–E curves for community net oxygen fluxes in each enclosure.

maximum mean irradiance was $550 \mu\text{mol m}^{-2} \text{s}^{-1}$ at midday (Fig. 2).

3.2. Sewage water characteristics

Mean ammonium concentration in sewage water was $1111 \mu\text{mol l}^{-1}$ (S.E. 213). Silicate concentration was also relatively high ($59.5 \mu\text{mol l}^{-1}$, S.E. 24.5), whereas phosphate ($151.5 \mu\text{mol l}^{-1}$, S.E. 24.5) and more evidently nitrate ($4.0 \mu\text{mol l}^{-1}$, S.E. 0.9) were in lesser concentrations.

3.3. Initial concentration of nutrients

Ammonium concentration in the enclosures was measured at the beginning of each incubation. Concentration in the control (enclosure 1) corresponded to ambient water ($0.67 \mu\text{mol l}^{-1}$, S.E. 0.43), whereas concentrations in the other enclosures resulted both from natural ammonium and added ammonium chloride. Total ammonium concentration was $5.17 \mu\text{mol l}^{-1}$ (S.E. 0.45) and $14.58 \mu\text{mol l}^{-1}$ (S.E. 0.53) in enclosures 2 and 3, respectively. Initial silicon concentrations with an average value of $5.25 \mu\text{mol l}^{-1}$ (S.E. 2.94) did not

Table 1

Estimated oxygen, carbon dioxide, ammonium and silicate fluxes in $\text{mmol m}^{-2} \text{day}^{-1}$ (SE are in parentheses)

Enclosure	Gross O ₂ production	Gross CO ₂ production	O ₂ respiration	CO ₂ respiration	NH ₄ uptake	Si(OH) ₄ uptake
1	33.17 (13.73)	32.20 (13.33)	36.96 (5.64)	42.13 (6.42)	0.680 (0.860)	0.277 (0.413)
2	49.01 (13.15)	47.58 (12.77)	56.40 (11.48)	64.30 (13.08)	1.603 (1.032)	0.757 (0.797)
3	66.65 (17.70)	64.71 (17.18)	86.88 (1.10)	99.04 (1.25)	2.134 (1.896)	1.582 (0.997)

Table 2

Curve fitting parameters for oxygen fluxes in each enclosure (SE are in parentheses)

Enclosure	<i>N</i>	F_{\max} (S.E.)	I_k (S.E.)	r (S.E.)	R^2
1	14	4.49 (0.56)	191.84 (66.82)	-1.78 (0.40)	0.89
2	13	5.85 (0.53)	133.91 (30.23)	-2.89 (0.49)	0.92
3	14	8.28 (0.63)	152.43 (35.91)	-4.16 (0.44)	0.95

significantly differ between enclosures (ANOVA, $F=0.07$, $n=48$, $p=0.92$).

3.4. Oxygen and CO₂ fluxes

Oxygen and CO₂ respiration (Table 1) calculated from in situ measurements after sunset, significantly differed for each enclosure (Kruskal–Wallis one-way analysis of variance, $P=0.02$). Community respiration was linearly related to initial concentration in the enclosure ($R^2=0.87$, ANOVA, $n=10$, $p=0.00$).

The curve-fitting parameters of oxygen fluxes at different light intensities (Fig. 3) are given in Table 2. F_{\max} in enclosure 3 was almost twice the value found in the control enclosure, enclosure 2 value being intermediate. F_{\max} estimates were linearly related to ammonium concentrations ($R^2=1.00$, ANOVA, $n=3$, $p=0.03$). Conversely, I_k was not significantly related to ammonium concentrations ($R^2=0.20$, ANOVA, $n=3$, $p=0.67$). Therefore, P_g values (Table 1) during 1 day, increased with ammonium enrichment. Calculated CO₂ production and measured CO₂ respiration were linearly related ($R^2=0.87$, ANOVA, $n=10$, $p=0.00$) with a slope (P/R) of 0.49 (S.E.=0.07).

3.5. Ammonium fluxes

Ammonium fluxes were more variable than oxygen fluxes (Fig. 3) as indicated by the lower

Table 3

Curve fitting parameters for ammonium fluxes in each enclosure (SE are in parentheses)

Enclosure	<i>N</i>	P_{\max} (S.E.)	I_k (S.E.)	k (S.E.)	R^2
1	16	-56.59 (20.38)	29.58 (34.89)	-12.60 (18.98)	0.38
2	15	-280.35 (58.22)	318.85 (152.54)	-50.04 (31.67)	0.78
3	15	-367.01 (46.06)	309.60 (90.31)	-28.98 (26.04)	0.90

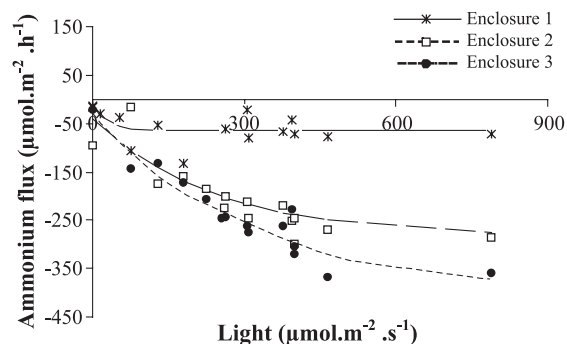


Fig. 4. Relationships between ammonium fluxes and light intensity in the three enclosures.

coefficients of determination of the curve-fit (Table 3). The total daily uptake (Table 1) was not significantly related to ammonium concentration ($R^2=0.86$, ANOVA, $n=3$, $p=0.24$). The fitting to P_g was higher but still not significant ($R^2=0.95$, ANOVA, $n=3$, $p=0.13$). A C/N flux ratio of 21 was derived from this regression. The ammonium fluxes described by the model were however characterized by a positive correlation with light intensity and a magnitude corresponding to initial ammonium concentrations (Fig. 4).

3.6. Silicate fluxes

Silicate fluxes were also irregular and displayed no significant rate of dissolution in dark conditions (Kruskal–Wallis test between the enclosures, $p=0.10$). The curve-fitting parameters (Table 4) indicated that Si dissolution at night was four times higher in enclosure 3 than in the control. The silicate flux from the sediment declined with increasing irradiance (Fig. 5) down to zero for irradiances greater than 300 $\text{mmol m}^{-2} \text{s}^{-1}$. Daily silicate uptake was linearly related to initial ammonium concentration ($R^2=1.00$, ANOVA, $n=3$, $p=0.04$); the

Table 4

Curve fitting parameters for silicate fluxes in each enclosure (SE are in parentheses)

Enclosure	<i>N</i>	F_{\max} (S.E.)	I_k (S.E.)	k (S.E.)	R^2
1	18	-30.30 (12.77)	97.83 (106.151)	38.64 (11.85)	0.27
2	13	-112.24 (37.33)	234.14 (193.73)	79.60 (20.30)	0.60
3	18	-199.34 (34.37)	158.69 (73.80)	192.25 (27.17)	0.72

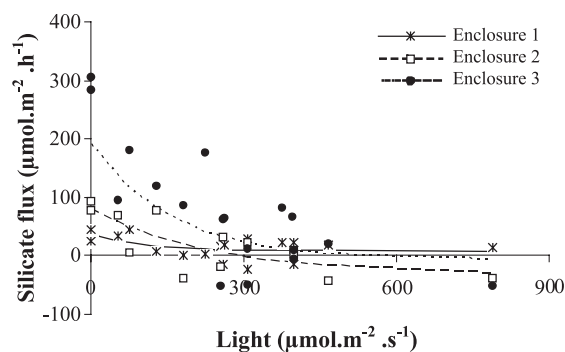


Fig. 5. Relationships between silicate fluxes and light intensity in the three enclosures.

significance being lower with P_g ($R^2=0.99$, ANOVA, $n=3$, $p=0.07$). A Si/C flux ratio of 0.04 was calculated.

4. Discussion

The use of flux chambers to assess benthic metabolism induces several perturbations in natural environment. In particular, diffusive fluxes at the water–sediment interface can be altered by hydrodynamics modifications generated by enclosures (Broström and Nilsson, 1999; Wenzhofer and Glud, 2002). Flux chambers also suppress particulate sedimentation from the water column, altering allochthonous organic matter input, hence the metabolic response of benthos. New techniques have been designed to limit such drawbacks for global metabolism assessments (Berg et al., 2003). However, the process of analysing and understanding the influence of fresh material deposition requires some control on environmental conditions. The use of mesocosms allows for such experimental developments, but at the cost of major alterations to the environment (Asmus et al., 1998; Kees Kersting and Lindblad, 2001; Laursen et al., 2002; Camacho and de Wit, 2003; Peralta et al., 2003). In situ experimentation in enclosures preserves sediment structure and associated biological communities. It remains, therefore, an important way for understanding the functioning of the benthos (Viollier et al., 2003).

Only ammonium was used to test the effects of nutrient concentration increase on benthic metabolism. Nitrate and phosphate are also important

contributors to the bottom-up control of marine primary production, especially in temperate environments (Tengberg et al., 2003) but ammonium is considered as the major inorganic N source for microphytobenthos (Welker et al., 2001; Cook et al., 2004) with turnover times of less than a day in tropical carbonate sediments (Capone et al., 1992). Furthermore, this choice was justified by the nutrient composition of both lagoon and urban sewage waters. Nitrate and phosphate concentrations were relatively low in the lagoon water. As the waste waters released around Noumea carried a strong load of ammonium, it was logically selected to act as an enrichment factor in our experiments.

Ammonium is generally regarded as the main factor limiting primary production in coral reef environments (Johnstone et al., 1989; Boucher et al., 1994). The present results strongly support the hypothesis that an increase in ammonium inputs immediately enhances microphytobenthos primary production. At an ambient concentration as high as $14.5 \mu\text{mol l}^{-1}$, ammonium was still a limiting factor for primary production. Previous studies in the SW New Caledonia lagoon have established a linear relationship between ammonium fluxes and ammonium initial concentration in enclosures, of up to $20 \mu\text{mol l}^{-1}$, values close to interstitial water concentrations (Boucher et al., 1994). The lower concentrations tested in our experiments confirm this general statement. Ammonium uptake rates proportional to concentrations were reported for microatolls (Steven and Atkinson, 2003). In the same way, an increase in community gross production has been observed during experiments on coral reef sediment enriched par NH_4^+ in an indoor aquarium room (Uthicke, 2001), and by holothurians excretion in laboratory and on the Great Barrier Reef (Uthicke and Klumpp, 1997, 1998). They showed that the production of benthic microalgae in coral reef environment is limited by the availability of inorganic nitrogen. These experiments were however carried out for at least 24 h and our results prove that microalgal production is enhanced for short-term ammonium pulses.

Typically, the New Caledonia SW lagoon is fuelled by oceanic water which maintains low nutrient concentrations. Light intensities are high in shallow tropical environment but not enough to induce photoinhibition of benthic communities (Clavier and

Garrigue, 1999; Underwood, 2002). Therefore, the system is not light limited and photosynthesis by microphytobenthos mainly depends on nutrients availability. Production enhancement is related to an increase in F_{\max} (the maximal production), which is linearly correlated to ammonium concentrations, when I_k (the optimal irradiance) does not change. The increase of F_{\max} with ammonium availability may be related to the multiplication of microphytobenthos cells in the sediment or to an enhanced photosynthesis process. A significant increase in microalgal biomass as estimated by sediment Chl *a* concentrations was observed during 7-day experimental laboratory exposures to elevated levels of inorganic nitrogen (Dizon and Yap, 1999). Such an increase in biomass is however unlikely to occur during our short-term incubations. At the study site, the microphytobenthos biomass (Chl *a*) was within the range known for the lagoon; chlorophyll *a* concentration in the top centimetre being close to the mean value (47.2 mg m⁻², S.E. 1.2) estimated for the whole lagoon (Garrigue, 1998). To limit experimental disturbance, sediment cores were collected at the end of each incubation to measure microphytobenthos biomass. The biomass assessment in the top centimetre of sediment would have been hampered by migration behaviour of diatoms within the sediment. Significant chlorophyll *a* concentration has been detected several centimetres under the interface, whereas only the top sediment layers receive enough light to achieve photosynthesis (Saburova and Polikarpov, 2003). Migration of diatoms towards the water–sediment interface in favourable conditions is therefore liable to increase the number of plant cells involved in photosynthesis process (Perkins et al., 2002; Underwood, 2002; Mundree et al., 2003). As a result, primary production can be increased without a noticeable change in total microphytobenthos biomass within the sediment.

Silicon is present in sea water as silicic acid Si(OH)₄, mainly used by diatoms for pelagic and benthic primary production. Diatom associated silicon corresponds to biogenic silica (BSi). Whether it derives from phytoplankton sedimentation or benthic primary production, BSi accumulates in sediments. Its delayed dissolution can be, in return, an important factor in pelagic diatom production (Ragueneau et al., 2002). The taxonomic composition of microphyto-

benthos assemblages at the study site is still unknown. The enhancement of silicate fluxes with increased light intensity suggests a multiplication of diatoms when ammonium concentration increases. The silicification of diatom cells are therefore considered to be independent from C and N incorporation, and the process can be achieved at night (Claquin et al., 2002). The present results indicate, however, increased BSi incorporation when ammonium is available. The biofilm at the water sediment interface is therefore likely to modify the solute exchange rates between the sediment and overlying water column (Srithongouthai et al., 2003).

The initial silicon concentration in the water was 5.25 μmol l⁻¹ during the experiments. Such a concentration is markedly lower than BSi solubility in water (Dixit et al., 2001). It is thus not surprising that fluxes from the sediment to the water column are observed at night and correspond to BSi dissolution. When irradiance increases, BSi fluxes are intercepted by the diatom biofilm (Srithongouthai et al., 2003) and silicon fluxes at the water–sediment interface decrease and even reverse. Therefore, during the cool season, sediments act as a source of silicon to the water column and may control the pelagic primary production by diatoms (Ragueneau et al., 2002). Ammonium contribution indirectly reduces this flux at the interface, but minor consequences are expected for pelagic production because of the relatively high silicon concentration in urban waste water.

Respiration was assessed shortly after nightfall so estimated values derive not only from a single experiment but represent the metabolic response of sediments after three 1.5 h successive incubations with light. The mineralization of organic matter is fast in tropical coastal environments (Yamamoto et al., 2001). Respiration represents the contribution of both microphytobenthos and heterotrophic organisms. The latter can use excess of floral biomass, but also the exopolymer produced by microphytes, which represents a biological source of labile carbon (Yallop et al., 2000; Perkins et al., 2001; Underwood, 2002; Wolfstein et al., 2002). In addition to enhancing benthic primary production, ammonium enrichment, even over short periods, increases the energy available to heterotrophs from microphytobenthos production.

Nutrient increase not only stimulates photoautotrophic production but also increases the rate of nitrifica-

tion by benthic bacteria, using ammonium as metabolic substrate (Eyre and Ferguson, 2002; Hewson et al., 2003) and CO₂ as carbon source. The enhancement in metabolism due to an increase in ammonium availability is therefore not only linked to organic matter input by primary production, but also stimulates bacteria able to grow chemolithotrophically (Madigan et al., 2000). Hence, the oxygen balance related to the ratio of plant production vs. community demand is reduced when ammonium concentration increases.

Such a result supports the known spatial distribution of benthic production in the SW lagoon of New Caledonia (Clavier and Garrigue, 1999). Benthic communities located near the reef in oligotrophic conditions are typically autotrophic with optimal nutrient recycling. Conversely, littoral sediments require an allochthonous energy or nutrient supply for their metabolic requirements. Therefore, in the study area, even pulses of urban waste waters resulted in a decrease of plant-related autotrophy in benthic communities.

Acknowledgements

This work was supported by the French Coastal Environment National Program (PNEC) and the IRD CAMELIA Research Unit. Authors are indebted to Dr. Tim O'Hara for correcting their English text. [SS]

References

- Asmus, R.M., Jensen, M.H., Jensen, K.M., Kristensen, E., Asmus, H., Wille, A., 1998. The role of water movement and spatial scaling for measurement of dissolved inorganic nitrogen fluxes in intertidal sediments. *Estuar. Coast. Shelf Sci.* 46, 221–232.
- Berg, P., Røy, H., Janssen, F., Meyer, V., Jørgensen, B.B., Huettel, M., de Beer, D., 2003. Oxygen uptake by aquatic sediments measured with a novel non-invasive eddy-correlation technique. *Mar. Ecol. Prog. Ser.* 261, 75–83.
- Bokn, T.L., Duarte, C.M., Pedersen, M.F., Marba, N., Moy, F.E., Barron, C., Bjerkeng, B., Borum, J., Christie, H., Engelbert, S., Fotel, F.L., Hoell, E.E., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Olsen, M.A., Sanderud, K.A., Sommer, U., Sorensen, K., 2003. The response of experimental rocky shore communities to nutrient additions. *Ecosystems* 6, 577–594.
- Boucher, G., Clavier, J., 1990. Contribution of benthic biomass to overall metabolism in New Caledonia lagoon sediments. *Mar. Ecol. Prog. Ser.* 64, 271–280.
- Boucher, G., Clavier, J., Garrigue, C., 1994. Estimation of bottom ammonium affinity in the New Caledonia lagoon. *Coral Reefs* 13, 13–19.
- Boucher, G., Clavier, J., Hily, C., Gattuso, J.P., 1998. Contribution of soft-bottoms to the community metabolism (primary production and calcification) of a barrier reef flat (Moorea, French Polynesia). *J. Exp. Mar. Biol. Ecol.* 225, 269–283.
- Bowen, J.L., Valiela, I., 2001. The ecological effects of urbanization of coastal watersheds: historical increases in nitrogen loads and eutrophication of Waquoit Bay estuaries. *Can. J. Fish. Aquat. Sci.* 58, 1489–1500.
- Broström, G., Nilsson, J., 1999. A theoretical investigation of the diffusive boundary layer in benthic flux chamber experiments. *J. Sea Res.* 42, 179–189.
- Bujan, S., Grenz, C., Fichez, R., Douillet, P., 2000. Evolution saisonnière du cycle biogéochimique dans le lagon sud-ouest de Nouvelle-Calédonie. Application d'un modèle compartimental. *C. R. Acad. Sci., Paris* 323, 225–233.
- Camacho, A.J., de Wit, R., 2003. Effect of nitrogen and phosphorus additions on a benthic microbial mat from a hypersaline lake. *Aquat. Microb. Ecol.* 32, 261–273.
- Capone, D.G., Dunham, S.E., Horrigan, S.G., Duguay, L.E., 1992. Microbial nitrogen transformations in unconsolidated coral reef sediments. *Mar. Ecol. Prog. Ser.* 80, 75–88.
- Chardy, P., Chevillon, C., Clavier, J., 1988. Major benthic communities of the south-west lagoon of New Caledonia. *Coral Reefs* 7, 69–75.
- Chifflet, S., Gérard, P., Fichez, R., 2003. Manuel d'analyses chimiques dans l'eau de mer. In: IRD (Ed.), Notes Tech.: Sci. Mer, Nouméa, p. 81.
- Claquin, P., Martin-Jézéquel, V., Kromkamp, J.C., Veldhuis, M.J.W., Kraay, G.W., 2002. Uncoupling of silicon compared with carbon and nitrogen metabolisms and the role of the cell cycle in continuous cultures of *Thalassiosira pseudonana* (Bacillariophyceae) under light, nitrogen, and phosphorus control. *J. Phycol.* 38, 922–930.
- Clavier, J., Garrigue, C., 1999. Annual sediment primary production and respiration in a large coral reef lagoon (SW New Caledonia). *Mar. Ecol. Prog. Ser.* 191, 79–89.
- Clavier, J., Boucher, G., Garrigue, C., 1994. Benthic respiratory and photosynthetic quotients in a tropical lagoon. *C. R. Acad. Sci., Paris* 317, 937–942.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210, 223–253.
- Collos, Y., 1987. Simultaneous uptake of nitrate, nitrite, ammonium and urea by microphytobenthos in the Lauzeries Channel during summer. 2nd Soviet–French Symposium on Production and Trophic Relationships. IFREMER, Yalta, pp. 215–220.
- Cook, P.L.M., Revill, A.T., Butler, E.C.V., Eyre, B.D., 2004. Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary: II. Nitrogen cycling. *Mar. Ecol. Prog. Ser.* 280, 39–54.
- de Casabianca, M.-L., Laugier, T., Marinho-Soriano, E., 1997. Seasonal changes of nutrients in water and sediment in a Mediterranean lagoon with shellfish farming activity (Thau Lagoon, France). *ICES J. Mar. Sci.* 54, 905–916.

- de Jonge, V.N., 1990. Response of the Dutch Wadden Sea ecosystem to phosphorus discharges from the River Rhine. In: McLusky, D.S., de Jonge, V.N., Pomfret, J. (Eds.), 18th Symp. of the Estuarine and Brackish-water Sciences Association: North Sea Estuaries Interactions. Hydrobiologia suppl., pp. 49–62.
- Dixit, S., Van Cappellen, P., van Bennekom, A.J., 2001. Processes controlling solubility of biogenic silica and pore water build-up of silicic acid in marine sediments. Mar. Chem. 73, 333–352.
- Dizon, R.M., Yap, H.T., 1999. Short-term responses of coral reef microphytobenthic communities to inorganic nutrient loading. Limnol. Oceanogr. 44, 1259–1267.
- Dizon, R.M., Yap, H.T., 2003. Metabolic changes and compositional shifts in nutrient-enriched tropical reef sediment communities. Sci. Mar. 67, 117–127.
- Douillet, P., 1998. Tidal dynamics of the south-west lagoon of New Caledonia: observations and 2D numerical modelling. Oceanol. Acta 21, 69–79.
- Douillet, P., Ouillon, S., Cordier, E., 2001. A numerical model for fine suspended sediment transport in the southwest lagoon of New Caledonia. Coral Reefs 20, 361–372.
- Duarte, C., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41, 113–136.
- Eyre, B.D., Ferguson, A.J.P., 2002. Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrification in seagrass, phytoplankton, benthic microalgae and macroalgae-dominated warm-temperate Australian lagoons. Mar. Ecol. Prog. Ser. 229, 43–59.
- Fanning, G.O., Pilson, M.E.Q., 1973. On the spectrophotometric determination of dissolved silica in natural waters. Anal. Chem. 45, 136–140.
- Fong, P., Fong, J.J., Fong, C.R., 2004. Growth, nutrient storage, and release of dissolved organic nitrogen by *Enteromorpha intestinalis* in response to pulses of nitrogen and phosphorus. Aquat. Bot. 78, 83–95.
- Garrigue, C., 1998. Distribution and biomass of microphytes measured by benthic chlorophyll *a* in a tropical lagoon (New Caledonia, South Pacific). Hydrobiologia 385, 1–10.
- Garrigue, C., DiMatteo, A., 1991. La biomasse végétale benthique du lagon sud-ouest de Nouvelle-Calédonie. Résultats bruts : liste taxonomique, biomasses, pigments chlorophylliens. Nouméa. ORSTOM. Arch. Sci. Mer. Biol. Mar., p. 143.
- Gattuso, J.P., Pichon, M., Delesalle, B., Canon, C., Frankignoulle, M., 1996. Carbon fluxes in coral reefs: I. Lagrangian measurement of community metabolism and resulting air–sea CO₂ disequilibrium. Mar. Ecol. Prog. Ser. 145, 109–121.
- Grall, J., Chauvaud, L., 2002. Marine eutrophication and benthos: the need for new approaches and concepts. Glob. Chang. Biol. 8, 83–830.
- Graneli, E., Sundbäck, K., 1985. The response of planktonic and microbenthic algal assemblages to nutrient enrichment in shallow coastal waters, southwest Sweden. J. Exp. Mar. Biol. Ecol. 85, 253–268.
- Grigg, R.W., 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. Mar. Ecol. Prog. Ser. 103, 25–34.
- Hatcher, B.G., Johannes, R.E., Robertson, A.I., 1989. Review of research relevant to the conservation of shallow tropical marine ecosystems. Oceanogr. Mar. Biol. 27, 337–414.
- Hewson, I., Vargo, G.A., Fuhrman, J.A., 2003. Bacterial diversity in shallow oligotrophic marine benthos and overlying waters: effects of virus infection, containment, and nutrient enrichment. Microb. Ecol. 46, 322–336.
- Invers, O., Kraemer, G.P., Pérez, M., Romero, J., 2004. Effects of nitrogen addition on nitrogen metabolism and carbon reserves in the temperate seagrass *Posidonia oceanica*. J. Exp. Mar. Biol. Ecol. 303, 97–114.
- Irigoin, X., Castel, J., 1997. Light limitation and distribution of chlorophyll pigments in a highly turbid estuary: the Gironde (SW France). Estuar. Coast. Shelf Sci. 44, 507–517.
- Johnstone, R., Koop, K., Larkum, V., 1989. Fluxes of inorganic nitrogen between sediments and water in a coral reef lagoon. Proc. Linn. Soc. N. S. W. 110, 219–227.
- Kees Kersting, K., Lindblad, C., 2001. Nutrient loading and metabolism in hard-bottom littoral mesocosms. Cont. Shelf Res. 21, 2117–2125.
- Kérouel, R., Aminot, A., 1997. Fluorometric determination of ammonia in sea and estuarine waters by direct segmented flow analysis. Mar. Chem. 57, 265–275.
- Koop, K., Booth, D., Broadbent, A., Brodie, J., Bucher, D., Capone, D.G., Coll, J., Dennison, W., Erdmann, M., Harrison, P.J., Hoegh-Guldberg, O., Hutchings, P., Jones, G.B., Larkum, A.W.D., O’Neil, J., Steven, A., Tentori, E., Ward, S., Williamson, J., Yellowlees, D., 2001. ENCORE: the effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. Mar. Pollut. Bull. 42, 91–120.
- Kromkamp, J., Peene, J., Van Rijswijk, P., Sandee, A., 1995. Nutrients, light and primary production by phytoplankton and microphytobenthos in the eutrophic, turbid Westerschelde Estuary (The Netherlands). Hydrobiologia 311, 9–19.
- Kuffner, I.B., Paul, V.J., 2001. Effects of nitrate, phosphate and iron on the growth of macroalgae and benthic cyanobacteria from Cocos Lagoon, Guam. Mar. Ecol. Prog. Ser. 222, 63–72.
- Labrosse, P., Fichez, R., Farman, R., Adams, T., 2000. New Caledonia. In: Sheppard, C. (Ed.), Seas at the Millennium, An Environmental Evaluation. Elsevier, Amsterdam, pp. 423–736.
- Laursen, A.E., Seitzinger, S.P., Dekorsey, R., Sanders, J.G., Breitburg, D.L., Osman, R.W., 2002. Multiple stressors in an estuarine system: effects of nutrients, trace elements, and trophic complexity on benthic photosynthesis and respiration. Estuaries 25, 57–69.
- Lorenzen, C.J., 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnol. Oceanogr. 12, 343–346.
- Madigan, M.T., Martinko, J.M., Parker, J., 2000. Brock Biology of Microorganisms. Prentice Hall, Upper Saddle River, NJ.
- Miyajima, T., Suzumura, M., Umezawa, Y., Koike, I., 2001. Microbiological nitrogen transformation in carbonate sediments of a coral-reef lagoon and associated seagrass beds. Mar. Ecol. Prog. Ser. 217, 273–283.
- Mundree, S., Perissinoto, R., Nozais, C., 2003. Seasonal variations in the vertical distribution of benthic microalgae in the upper

- sediment of the Mdloti estuary, South Africa. *Bot. Mar.* 46, 323–331.
- Naim, O., 1993. Seasonal responses of a fringing reef community to eutrophication (Reunion Island, Western Indian Ocean). *Mar. Ecol. Prog. Ser.* 99, 137–151.
- Pastorok, R.A., Bilyard, G.R., 1985. Effects of sewage pollution on coral reefs communities. *Mar. Ecol. Prog. Ser.* 21, 175–189.
- Paterson, D.M., Crawford, R.M., Little, C., 1986. The structure of benthic diatom assemblages: a preliminary account of the use and evaluation of low-temperature scanning electron microscopy. *J. Exp. Mar. Biol. Ecol.* 95, 279–289.
- Peralta, G., Bouma, T.J., van Soelen, J., Pérez-Lloréns, J.L., Hernández, I., 2003. On the use of sediment fertilization for seagrass restoration: a mesocosm study on *Zostera marina* L. *Aquat. Bot.* 75, 95–110.
- Perkins, R.G., Underwood, G.J.C., Brotas, V., Snow, G.C., Jesus, B., Ribeiro, L., 2001. Responses of microphytobenthos to light: primary production and carbohydrate allocation over an emersion period. *Mar. Ecol. Prog. Ser.* 223, 101–112.
- Perkins, R.G., Oxborough, K., Hanlon, A.R.M., Underwood, G.J.C., Baker, N.R., 2002. Can chlorophyll fluorescence be used to estimate the rate of photosynthetic electron transport within microphytobenthic biofilms? *Mar. Ecol. Prog. Ser.* 228, 47–56.
- Philippart, C.J.M., Cadée, G.C., 2000. Was total primary production in the western Wadden Sea stimulated by nitrogen loading? *Helgol. Mar. Res.* 54, 55–62.
- Ragueneau, O., Chauvaud, L., Leynaert, A., Thouzeau, G., Paulet, Y.M., Bonnet, S., Lorrain, A., Grall, J., Corvaisier, R., Le Hir, M., Jean, F., Clavier, J., 2002. Direct evidence of a biologically active coastal silicate pump: ecological implications. *Limnol. Oceanogr.* 47, 1849–1854.
- Rizzo, W.R., 1990. Nutrient exchanges between the water column and a subtidal benthic microalgal community. *Estuaries* 13, 219–226.
- Saburova, M.A., Polikarpov, I.G., 2003. Diatom activity within soft sediments: behavioural and physiological processes. *Mar. Ecol. Prog. Ser.* 251, 115–126.
- Srithongouthai, S., Sonoyama, Y.I., Tada, K., Montani, S., 2003. The influence of environmental variability on silicate exchange rates between sediment and water in a shallow-water coastal ecosystem, the Seto Inland Sea, Japan. *Mar. Pollut. Bull.* 47, 10–17.
- Steven, A.D.L., Atkinson, M.J., 2003. Nutrient uptake by coral-reef microatolls. *Coral Reefs* 22, 197–204.
- Sundbäck, K., Jönsson, B., 1988. Microphytobenthic productivity and biomass in sublittoral sediments of a stratified bay, southeastern Kattegat. *J. Exp. Mar. Biol. Ecol.* 122, 63–81.
- Tengberg, A., Almroth, E., Hall, P., 2003. Resuspension and its effects on organic carbon recycling and nutrient exchange in coastal sediments: in situ measurements using new experimental technology. *J. Exp. Mar. Biol. Ecol.* 285–286, 119–142.
- Tyler, A.C., McGlathery, K.J., Anderson, I.C., 2003. Benthic algae control sediment–water column fluxes of organic and inorganic nitrogen compounds in a temperate lagoon. *Limnol. Oceanogr.* 48, 2125–2137.
- Underwood, G.J.C., 2002. Adaptations of tropical marine microphytobenthic assemblages along a gradient of light and nutrient availability in Suva Lagoon, Fiji. *Eur. J. Phycol.* 37, 449–462.
- Uthicke, S., 2001. Interactions between sediment-feeders and microalgae on coral reefs: grazing losses versus production enhancement. *Mar. Ecol. Prog. Ser.* 210, 125–138.
- Uthicke, S., Klumpp, D.W., 1997. Ammonium excretion by holothurians enhances production and turnover of benthic diatom communities. 8th Int. Coral Reef Sym. Smithsonian Tropical Reserach Institute, Balboa, Republic of Panama, Panama, pp. 873–876.
- Uthicke, S., Klumpp, D.W., 1998. Microphytobenthos community production at a near-shore coral reef: seasonal variation and response to ammonium recycled by holothurians. *Mar. Ecol. Prog. Ser.* 169, 1–11.
- Valiela, I., Foreman, K., Lamontagne, M., Hersh, D., Costa, J., Peckol, P., Demeo-Anderson, B., D'Avanzo, C., Babione, M., Sham, C.H., Brawley, J., Lajtha, K., 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. *Estuaries* 15, 443–457.
- Viollier, E., Rabouille, C., Apitz, S.E., Breuer, E., Chaillou, G., Dedieu, K., Furukawa, Y., Grenz, C., Hall, P., Janssen, F., Morford, J.L., Poggiale, J.C., Roberts, S., Shimmield, D., Taillefert, M., Tengberg, A., Wenzhöfer, F., Witt, U., 2003. Benthic biogeochemistry: state of the art technologies and guidelines for the future of in situ survey. *J. Exp. Mar. Biol. Ecol.* 285–286, 5–31.
- Welker, C., Sdrigotti, E., Covelli, S., Faganeli, J., 2001. Microphytobenthos in the Gulf of Trieste (Northern Adriatic Sea): relationship with labile sedimentary organic matter and nutrients. *Estuar. Coast. Mar. Sci.* 55, 259–273.
- Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* 30, 377–392.
- Wenzhofer, F., Glud, R.N., 2002. Benthic carbon mineralization in the Atlantic: a synthesis based on in situ data from the last decade. *Deep-Sea Res., Part I* 49, 1255–1279.
- Wolfstein, K., de Brouwer, J.F.C., Stal, L.J., 2002. Biochemical partitioning of photosynthetically fixed carbon by benthic diatoms during short-term incubations at different irradiances. *Mar. Ecol. Prog. Ser.* 245, 21–31.
- Yallop, M.L., Paterson, D.M., Wellsbury, P., 2000. Interrelationships between rates of microbial production, exopolymer production, microbial biomass, and sediment stability in biofilms of intertidal sediments. *Microb. Ecol.* 39, 116–127.
- Yamamoto, M., Kayanne, H., Yamamuro, M., 2001. Characteristics of organic matter in lagoonal sediments from the Great Barrier Reef. *Geochem. J.* 35, 385–401.