Coral Reefs (1994) 13:13–19

Coral Reefs

Estimation of bottom ammonium affinity in the New Caledonia lagoon

G. Boucher[1], J. Clavier[2] and C. Garrigue[2]

[1] URA CNRS 699 Biologie des Invertébrés Marins MNHN, 55 rue Buffon, 75231 Paris, France
[2] Centre ORSTOM de Nouméa, BP A5 Nouvelle-Calédonie

Accepted 23 October 1992

Abstract. Ammonium affinity of New Caledonia lagoon benthic communities was measured during the course of 33 *in situ* enrichment experiments, in order to estimate the contribution of benthos to ammonium fluxes. Ammonium chloride was injected into enclosures pushed into the sediment, in order to obtain a concentration of 20–22 $\mu mol\,l^{-1}$ in the enclosed water which approximated the interstitial water content. Ammonium kinetic uptake was then followed for two hours. Grey-sand bottom displayed the highest affinity for ammonium, but white-sand and muddy bottom affinity was of the same order of magnitude. Macrophytes, and microphytes (when macrophytes are absent), account for the bulk of ammonium bottom uptake. As a result, grey-sand bottoms with their dense macrophyte cover represent a sink for water column nitrogen and play a key role in nutrient cycling of the lagoon.

Introduction

Despite the low levels of nutrients in reef waters (Crossland 1983) benthic communities have a high productivity (Larkum 1983). Consequently, one of the most important problems facing coral reef biology is the question of nutrient limitation of organic matter production (Atkinson 1988). Are benthic communities operating near their upper production limit set by metabolic rates associated with the photosynthetic processes, or are they nutrient depleted (Grigg et al. 1984)? Nitrogen fixation (Wiebe et al. 1975) and endo-upwelling (Rougerie and Wauthy 1986) could ease the problem by increasing nutrient availability in oligotrophic environments. The nutrient limitation hypothesis has been tested by fertilization experiments (Kinsey and Domm 1974; Hatcher and Larkum 1983). The conclusion was that long-term nutrient enrichments can at best produce relatively small increases in the rate of net community photosynthesis and plant biomass, but little increase in community respiration. It may be that nutrient limitation is of less significance than formerly believed, and other factors could control primary productivity (Grigg et al. 1984; Capblancq 1990). In low nutrient environments, production depends mostly on internal mechanisms which act to recycle the limiting nutrient. In the lagoons of coral reef ecosystems, re-mineralization of organic inputs to the sediments is a potentially important pathway of recycling (Kinsey 1985).

Our previous results in the SW New Caledonia lagoon indicated that benthic/pelagic coupling is low when compared to temperate ecosystems (Clavier et al. 1990; Boucher and Clavier 1990). The ammonium and nitrate efflux, and even dissolved organic nitrogen uptake at the water-sediment interface, are too insignificant to account for the mineralization of a large amount of organic matter (mean net deposition: $0.84\,gC\,m^{-2}\,d^{-1}$ on an annual basis (Chardy and Clavier 1988)). Nutrient-poor conditions are generally described for interstitial water of coral reef sediments (Williams et al. 1985; Corredor and Capone 1985). Active uptake of ammonium chloride against the concentration gradient has been demonstrated in Great Barrier Reef sediments (Johnstone et al. 1989). Uptake occurring during enrichment experiments was attributed to microbial processes and to utilization by microphytes in the uppermost layers of the sediment.

In this paper, we experimentally evaluate the short-term rates of nitrogen uptake by benthic communities in the SW New Caledonia lagoon in order to determine if the sedimentary benthos is a source or a sink for dissolved ammonium in lagoon waters. We also partition the factors controlling flux rates at the water/bottom interface to estimate the benthos contribution to the biological uptake of nitrogen. We use the term "affinity" for ammonium uptake in enrichment experiments in its simplest meaning, i.e. ability of an organism or a complex community to transport nutrient (Button 1986).

Material and methods

Study site

During a cruise on board OV Alis, ammonium enrichments were investigated at 12 stations (Fig. 1) in the SW New Caledonia lagoon from 16th July to 2nd August 1990 (Clavier et al. 1991). Sampling

Correspondence to: G. Boucher

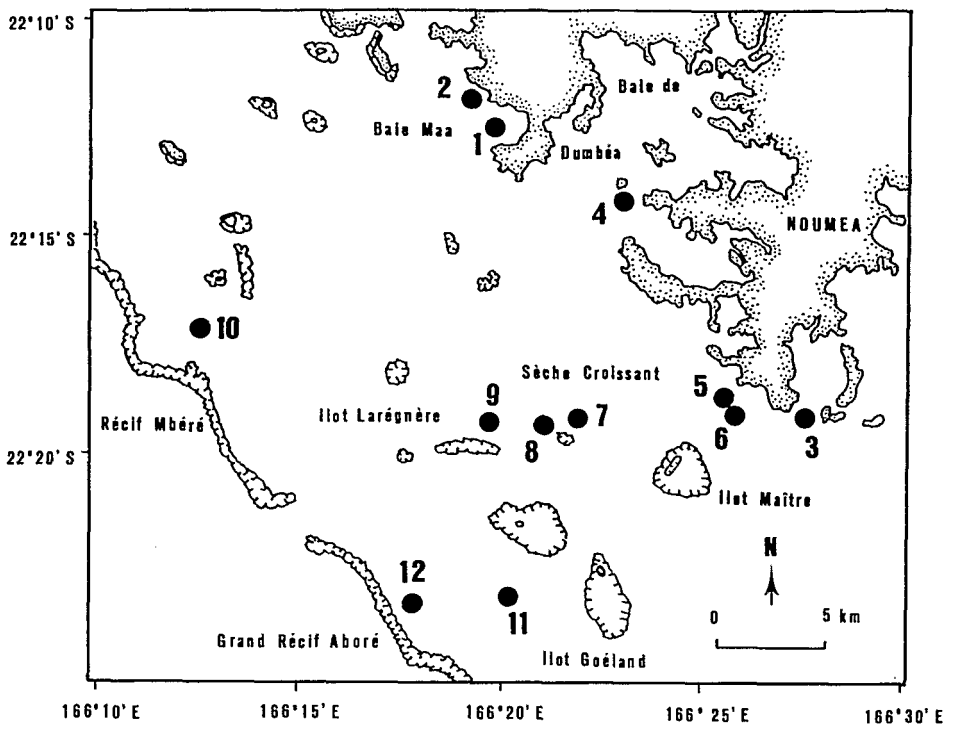

Fig. 1. Location of sampling stations in the southwest lagoon of New Caledonia. Muddy bottoms: 1 = Baie Maa 1 (Z = 13 m), 2 = Baie Maa 2 (Z = 12 m), 3 = Baie Sainte Marie (Z = 13 m); Grey-sand bottoms: 4 = Ilot Freycinet (Z = 9 m), 5 = Rocher à la Voile I (Z = 10 m), 6 = Rocher à la Voile 2 (Z = 9 m), 7 = Sèche Croissant 2 (Z = 11 m, test station), 8 = Ilot Signal (Z = 16 m), 9 = Ilot La Régnère (Z = 16 m); White-sand bottoms: 10 = Récif Mbéré 3 (Z = 12 m), 11 = Ilot Goéland (Z = 12 m), 12 = Grand Récif Aboré (Z = 16 m)

sites were located in communities previously defined as muddy bottoms, grey-sand bottoms, and white-sand bottoms [relative surface area: 35, 50, 15% respectively (Chardy et al. 1988)]. At each station, triplicate enclosure experiments were performed during morning hours, when light was still increasing. Water temperature ranged from 24 to 25 °C and water depth from 8.6 to 15.4 m (mean: 12.5 m).

A grey-sand station (Sèche Croissant 2), which displayed the highest ammonium flux in previous experiments (Boucher et al. 1990) and the densest macrophyte cover, was investigated to determine ammonium content in interstitial water. Selection of a suitable ammonium concentration for injection in the enclosures could then be made.

Incubation procedure

Variations of oxygen and ammonium concentrations were measured in the circulating water trapped in dark or clear acrylic enclosures pushed into the sediment (50 cm diameter, volume 50–60 l depending on core depth), according to a procedure described by Boucher and Boucher-Rodoni (1988) and Boucher and Clavier (1990). A calibrated polarographic electrode connected to a submersible container was placed on the recirculating close-circuit system of each enclosure for continuous oxygen recording (Yellow Spring Instruments). Samples for ammonium analysis were withdrawn with 60 ml syringes, and external water was admitted through a port during sampling to avoid interstitial water release from the sediment.

Dark oxygen uptake and ammonium flux were first measured at the ambient ammonium concentration of the contained water for two hours. After water renewal in the enclosure (10 min), by reopening and reclosing the domes on the core inserted into the same sediment area, ammonium enrichment was performed with a syringe, through a port, by SCUBA divers. At the test station "Sèche Croissant 2", light uptake of NH_4Cl was estimated during the course of two successive series of triplicated incubations for two hours, on 2-8-90. Six concentrations were then tested to obtain ~ 0, 6, 12.5, 25, 50 and 100 µmol l^{-1} enrichments in the 50 litre enclosures. At other stations, only one concentration (25 µmol l^{-1}) was tested on triplicated enclosures.

Light ammonium kinetics was followed, at 5 min intervals in the first test experiment and at 20 min intervals in the other experiments in order to obtain bottom ammonium affinity with each enrichment level and bottom type. Some control experiments were performed in enclosures isolated from the benthos. For each enclosure, the rate of change in oxygen (mg O_2 m^{-2} h^{-1}) and ammonium (µmol m^{-2} h^{-1}) concentration, as a function of time, was calculated by linear regression of the 5–7 measures, normalized for water volume and for sediment surface area. Ammonium release to the water column was considered as positive and ammonium uptake or bottom affinity was considered as negative.

Processing of the samples

The interstitial water from the top five centimeters of replicate sediment cores (23 cm^2 diameter) collected by SCUBA divers was obtained by gravity and poured through a glass filter to obtain 20 ml filtrate. Ammonium content of interstitial water and other water column samples were immediately analyzed on board using the indo-phenol blue reaction (Solorzano 1969).

At the end of triplicated simultaneous incubations, three sediment cores (5.3 cm^2 diameter) were collected in each enclosure, for measurement of ATP content and photosynthetic pigment in the top centimeter. ATP (mg m^{-2}) was immediately extracted on board with 10 ml boiling $NaHCO_3$ (Bancroft et al. 1966) and the extract was deep-frozen for later analysis by the bioluminescence method (Charpy-Roubaud 1986). Pigments (mg m^{-2}) were extracted from the sediment in a refrigerator, after deep-freezing and lyophilisation, using 90% acetone for 18–24 h (Garrigue and Di Matteo 1990) and the extract was measured with a spectrophotometer (Lorenzen 1967). Macrophytes and macrofauna were collected from the enclosures by an air-lift apparatus with a 1 mm sieve net. Species composition and total biomass were analyzed in the laboratory after fixation (using 10% formalin), followed by dessication at 60 °C, and ash content determination at 550 °C.

Statistical treatment of the results

Non-parametric Kruskal-Wallis one-way analysis of variance (Siegel 1956) was used to test for differences between the three bottom types. Ammonium affinity was related to oxygen uptake in ambient water and biomass (considered separately as ATP, microphytobenthos, macroflora and macrofauna) using linear regressions. A stepwise multiple regression analysis (Sokal and Rohlf 1981) was performed on components of macrophyte biomass (seagrass, seaweeds and Corallinacea). Independence between the variables was first tested using linear regression.

Results

Raw data including sediment grain size, benthic parameters and flux measurements have been published elsewhere for each station (Clavier et al. 1991).

Sediment type and interstitial water

Sediment grain size was accepted as the main criterion to separate the stations in muddy bottoms (stations 1–3), grey-sand bottoms (stations 4–9), and white-sand bottoms (stations 10–12) according to Chardy et al. (1988). Ammonium concentration in interstitial water of the top five centimetres at the grey-sand station "Sèche Croissant 2" was constant for five replicates: $25.6 \pm 1.1\ \mu mol\ l^{-1}$ (s.e. = 0.6). We considered this concentration as the upper range of NH_4Cl to be injected into the water trapped in the enclosures, without inverting the diffusion gradient. This grey-sand station was known to display the highest ammonium efflux (Boucher and Clavier 1990, and present results) and therefore should have had the highest interstitial water content.

Ammonium uptake kinetics

Light was constant during the experiments: $128\ \mu E\ m^{-2}\ s^{-1}$. As the exact volume of the enclosures was greater than expected at the beginning of the experiments, due to lower core insertion into the substrate, the actual enrichments in the trapped water were less than calculated, i.e., 0, 5.4, 10.7, 21.1, 42.9, $85.6\ \mu mol\ l^{-1}$. When a volume of ambient water or of $25\ \mu mol\ l^{-1}$ enriched water was isolated from the sediment, no noticeable wall effects ammonium uptake in the water volume could be demonstrated inside the enclosure.

The light ammonium uptake rate measured at different levels of enrichment at the test station was not linear for concentration, but increased exponentially (up to 20 times between 5.4 and $42.9\ \mu mol\ l^{-1}$ and then stabilized at higher concentrations (Fig. 2). Uptake was consistent with Michaelis-Menten kinetics, but present results did not allow the calculation of significant kinetic parameters. A $25\ \mu mol\ l^{-1}$ enrichment fulfilled the requirement of a concentration range expected to approximate interstitial water content and to allow maximum uptake without saturation effects.

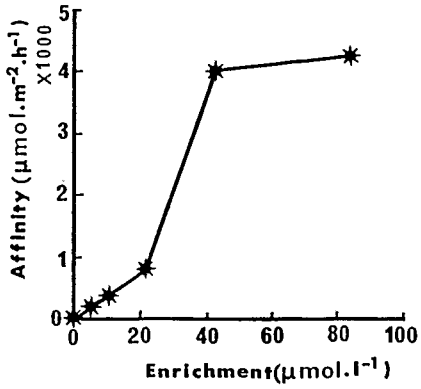

Fig. 2. Ammonium bottom affinity ($\mu mol\ N\text{–}NH_4\ m^{-2}\ h^{-1}$) at different levels of ammonium enrichment ($\mu mol\ N\text{–}NH_4\ Cl\ l^{-1}$). Data from the test station "Sèche Croissant 2" during 2 hour light incubations

Ammonium exchange in ambient water and enrichment experiments

Initial dark experiments on the same sediment area as the enrichment experiments allowed the measurement of *in situ* ammonium flux. Uptake or release between sediment and water column were low and erratic with rates ranging from -17.8 (s.e. = 2.4, $n = 7$), 12.5 (s.e. = 10.5, $n = 16$), 12.9 (s.e. = 10.8, $n = 7$) $\mu mol\ m^{-2}\ h^{-1}$ for muddy, grey-sand and white-sand bottoms, respectively. No significant differences of ammonium fluxes between bottom types could be demonstrated (Kruskal-Wallis test not significant, $P > 0.05$). Ammonium affinity was measured in 33 successful enrichment experiments in ambient light (Table 1). Uptake was found to be significantly different according to bottom type (Kruskal-Wallis test: $P < 0.01$). Ammonium uptake was generally far higher in grey-sand bottoms (580.8, $n = 17$, s.e. = 83.5 $\mu mol\ m^{-2}\ h^{-1}$) than in muddy bottoms (312.8, $n = 8$, s.e. = 39.8 $\mu mol\ m^{-2}\ h^{-1}$) and white-sand bottoms (334.4, $n = 8$, s.e. = 30.9 $\mu mol\ m^{-2}\ h^{-1}$). The latter two did not differ significantly.

Relation between ammonium uptake and oxygen flux

Respiration during dark incubations at ambient ammonium concentration ranged from 15.5 to $132.7\ mg\ O_2\ m^{-2}\ h^{-1}$. Oxygen uptake was similar at grey-sand bottom stations (58.8, $n = 17$, s.e. = $4.6\ mg\ O_2\ m^{-2}\ h^{-1}$) and at white-sand stations (52.7, $n = 8$, s.e. = $6.5\ mg\ O_2\ m^{-2}\ h^{-1}$), and significantly higher (Kruskal-Wallis test: $P < 0.03$) than at muddy bottom stations (37.0, $n = 9$, s.e. $4.6\ mg\ O_2\ m^{-2}\ h^{-1}$). Ammonium affinity in light enrichment experiments was linearly correlated with dark oxygen uptake in ambient water ($n = 33$, $r = 0.70$, $P < 0.001$) indicating that affinity is related to aerobic biological activity and not to chemosynthetic uptake.

Table 1. Mean values and standard errors (s.e.) of sediment parameters, oxygen uptake, ammonium flux and affinity, and benthic biomass at 12 investigated stations in the SW New-Caledonia lagoon. Station: station numbers in Fig. 1 (test station = 7); Silt = percentage of particles finer than 63 µm; Oxygen uptake ($mg\,m^{-2}\,h^{-1}$) = respiration in dark enclosures at ambient nutrient concentration ($n = 3$ except stations 4 and 11: $n = 2$); Ammonium flux = NH_4 ($\mu mol\,m^{-2}\,h^{-1}$) exchange in dark enclosures at ambient water concentration ($n = 3$ except stations 1: $n = 1$, 4: $n = 2$, 5: $n = 2$, 11: $n = 1$); Affinity = ammonium chloride bottom uptake ($\mu mol\ N\text{-}NH_4\,m^{-2}\,h^{-1}$) at 25 $\mu mol\,l^{-1}$ enrichment in light incubations ($n = 3$ except stations 1: $n = 2$, 4: $n = 2$, 11: $n = 2$); ATP = ATP content ($ng\,cm^{-2}$) in the first centimeter of sediment ($n = 3$); Chl a = sediment chlorophyll a content ($mg\,m^{-2}$) in the first centimeter of sediment ($n = 3$); Flora = macrophyte biomass ($g\,m^{-2}$ AFDW, $n = 3$); Fauna = macrofauna biomass = ($g\,m^{-2}$ AFDW, $n = 3$)

Bottom	Station	Silt	Oxygen uptake	s.e.	Ammonium flux	s.e.	Ammonium affinity	s.e.	ATP	s.e	Chl a	s.e.	Flora	s.e.	Fauna	s.e.
Muddy	1	36.9	31	13	29		−282	56	156	32	52	9	0	0	4.8	0.9
	2	14.4	16	7	−34	32	−226	42	200	47	20	1	0	0	6.2	8.3
	3	19.1	41	6	−17	6	−420	108	232	31	82	11	46.5	16.6	12.6	5.9
Grey-Sand	4	5.1	43	21	60	37	−504		268	80	84	19	18.1	7.6	44.8	18.9
	5	6.7	36	5	−55	8	−582	98	288	71	42	10	17.4	2	14.5	4.5
	6	6.4	43	20	37	9	−438	59	206	24	46	5	7.4	6.5	11.1	1.8
	7	6.2	88	33	2	16	−1151	463	331	42	27	8	47.1	24	14.4	9.6
	8	8.1	53	7	33	13	−545	142	318	44	20	4	29.9	5	12.3	12.4
	9	4.5	38	10	−8	46	−239	16	367	84	50	16	3.5	2.1	8.3	4.7
White-Sand	10	4.2	28	18	7	42	−310	140	394	30	24	8	0	0	1.6	1.1
	11	5.6	58	8	23		−393	24	484	73	71	21	0.9	0.9	6.3	3.6
	12	3.4	52	9	15	16	−320	46	460	42	50	9	0	0	3.1	1.8

Relation between ammonium uptake and benthic parameters

No significant correlation was observed between ammonium affinity and silt content ($r = -0.18$, $P = 0.31$), or mean grain size ($P = 0.10$, $P = 0.62$), a result suggesting that affinity is not controlled by physical and biological properties of the sediment related to grain size. Similarly, there was no observed relationship between ammonium uptake and ATP pool or macrofauna (Table 2), indicating that secondary production is not a dominant factor in ammonium uptake processes. However, ammonium uptake was strongly correlated with macrophyte biomass (Table 2). When calcareous algae (Corallinacea) were omitted from biomass evaluation, r improved to 0.91 with $P < 0.01$ (Fig. 3) indicating that these calcareous algae have a lower ammonium affinity compared to other macrophytes.

For the whole data set, ammonium uptake was not correlated with chlorophyll content in the top centimeter of sediment. Correlation coefficients become significant when calculated for white-sand bottom and muddy bottom stations alone (Table 2), demonstrating that microphytobenthos ammonium uptake becomes significant only when macrophytes are absent or reduced. Both groups of primary producers are thus responsible for bottom ammonium affinity. However, when stations with macrophytes were omitted (Fig. 4), cancelling the prevailing influence of macrophyte cover, bottom ammonium affinity was significantly correlated with chlorophyll content ($r = 0.65$, $P = 0.04$). The relationships with ATP and macrobenthos remained insignificant.

As macrophyte biomass is the only measured parameter significantly related to affinity at all sites in the lagoon, we performed a stepwise multilinear regression of ammonium affinity (VNH) on respective independent component biomasses: seaweeds without Corallinaceae (ALGAE); Corallinaceae alone; seagrasses (PHANERO):

$$VNH = 18.05\ ALGAE + 11.87\ PHANERO + 290.74$$
$$(r^2 = 0.85,\ P < 0.001)$$

The contribution of calcareous algae (Corallinaceae) was too low to be included by the model. The influence of macroalgae on bottom nutrient affinity appears more

Table 2. Relation between ammonium affinity and benthic parameters; n: number of measurements; r: linear correlation coefficient; P: probability level; ns: non significant; *: significant at $P < 0.05$; **: highly significant at $P < 0.01$

Parameters	Muddy bottoms			Grey sand bottoms			White sand bottoms			Whole lagoon		
	n	r	P	n	r	P	n	r	P	n	r	P
V NH/ATP	7	0.17	0.71 (ms)	17	0.07	0.77 (ns)	8	−0.18	0.66 (ns)	33	0.02	0.91 (ns)
V NH/Macrofauna	7	0.11	0.82 (ns)	17	0.08	0.77 (ns)	8	0.3	0.47 (ns)	33	0.26	0.14 (ns)
V NH/Macroflora	7	0.8	0.03 (*)	17	0.92	0.00 (**)	8	0.39	0.34 (ns)	33	0.73	0.00 (**)
V NH/Chlorophyll	7	0.78	0.04 (*)	17	−0.35	0.17 (ns)	7	0.84	0.02 (*)	33	−0.14	0.41 (ns)

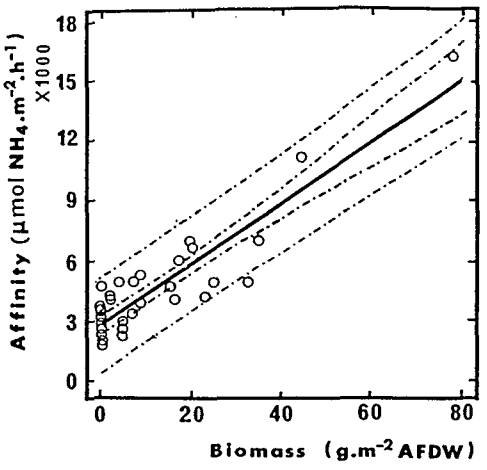

Fig. 3. Relationship between macrophyte biomass without Corallinacea ($g\,m^{-2}$ AFDW) and bottom affinity ($\mu mol\ N\text{-}NH_4\ Cl\ l^{-1}$); $n = 33$ experiments; $r = 0.91$; $P < 0.01$. Dashed lines = 95 and 99% confidence intervals

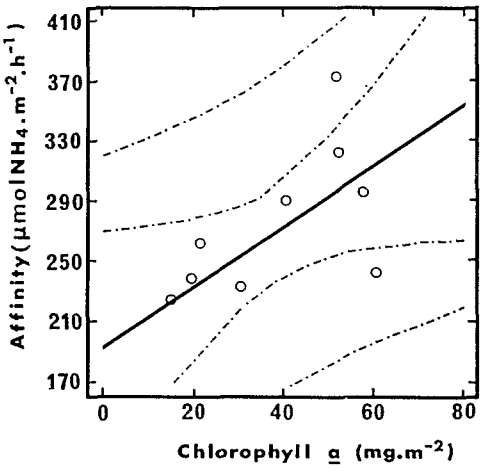

Fig. 4. Relationship between sediment chlorophyll a content ($mg\,m^{-2}$) and bottom ammonium affinity ($\mu mol\,m^{-2}\,h^{-1}$) at stations without any macrophyte cover ($n = 10$ experiments; $r = 0.65$; $P = 0.04$). Dashed lines = 95 and 99% confidence intervals

important than the influence of seagrass, although their respective biomasses ($5.79\,g\,m^{-2}$ and $4.84\,g\,m^{-2}$) were not significantly different ($t = 0.38$, $P = 0.72$).

Discussion

Ammonium uptake at the water-sediment interface was measured on a whole community, i.e. bottom-water and sediment with its living biomass (bacteria, microphytobenthos, macrophyte cover, meiofauna and macrofauna). Ammonium affinity may be the result of different processes such as adsorption (accumulation on a solid surface), or absorption (uptake by living biomass).

Exchangeable ammonium adsorption and desorption, between sediment particles and the water column, are known to be rapid (< 2 h) and linear with respect to concentrations from 1 to $10\,mmol\,l^{-1}$ (Rosenfeld 1979). The adsorption coefficient generally increases with decreasing grain size (Mackin and Aller 1984). No sterilized sediment controls were performed to assess adsorption, but our results demonstrate a non-significant relationship between ammonium affinity and granulometric parameters. Such a physical regulation of ammonium exchange does not appear to be a major process in the lagoon of New Caledonia.

We measured low ammonium exchanges in enclosure incubations performed in ambient oligotrophic waters. Our enrichment experiments allowed high bottom uptake despite an opposing concentration gradient in the underlying sediment, which indicates an active uptake process occurs in the top layers of sediments, as also found by Johnstone et al. (1989). Across living membranes, ion fluxes result (1) from passive diffusion (uptake proportional to external concentration) or (2) from facilitated diffusion, which allows transportation of solute down an electrochemical concentration gradient, and/or (3) from exchange diffusion which involves a carrier producing ion selectivity and saturation (DeBoer 1981). Such an active transport process moves a material across a membrane against a gradient, i.e. uptake is linked with metabolic processes and rates exhibit saturation kinetics following Michaelis-Menten equations. Our test experiments at "Sèche Croissant 2" station (Fig. 2) revealed a linear relation between uptake rate and external concentration up to $20\,\mu mol\,l^{-1}$ (which approximates the interstitial concentration) suggesting adsorption or diffusion at low concentrations. At higher concentration, active transport may have prevailed as suggested by the subsequent rapid increase and saturation kinetics between 20 and $100\,\mu mol\,l^{-1}$. At the 12 sampling stations, we measured ammonium kinetics that did not suggest enhanced initial ammonium uptake during the two hour incubations, and no saturation kinetics at the chosen enrichment concentration. At higher concentration and longer incubation time, Johnstone et al. (1989) observed saturation kinetics on fine and coarse sand from Great Barrier Reef.

The uptake of ammonium by the enclosed water was insignificant compared to benthos uptake, as demonstrated by our control experiments. As ammonium ions were not significantly adsorbed on the enclosure walls, the enrichment was mainly taken up or modified by sediment and/or benthic organisms in the top layers of the substrate.

A close coupling between dissolved nutrient efflux and bacterial productivity has been suggested by chamber experiments where antibiotics were added (Stanley et al. 1987; Boto et al. 1989). However, short-term organic enrichment in temperate ecosystems suggest that such eutrophication has no effect on bottom community respiration within 2 h (Van Es 1982), as found in our preliminary experiments. It is probable that bacterial populations are not able to immediately use the nitrogen supply, as suggested by the absence of any correlation between affinity and ATP content of sediments in our experiments. In contrast, the microphytobenthos is known to immediately control the nutrient influx or efflux at the water-sediment interface (Höpner and Wonneberger 1985; Andersen and Kristensen 1988; Sundbäck and Granéli

1988). Ammonium enrichments in oligotrophic lake sediments showed that oxygen production was stimulated by 36% after 5–6 h incubation, indicating microphyte nitrogen deficiency (Dodds and Priscu 1990). Our results show that the microphytobenthos regulates ammonium fluxes at water sediment interface, but to a far lower extent than macrophytes.

Seaweed ammonium saturation kinetics are known to be facilitated by diffusion or active transport (Raven 1976; Hanisak and Harlin 1978; D'Eila and DeBoer 1978). Ammonium uptake exceeds that of nitrate and no toxic effects were observed down to 30 $\mu mol\,l^{-1}$ (Haines and Wheeler 1978). The process is a function not only of external but also internal nitrogen concentration (D'Eila and DeBoer 1978). This implies that seaweeds living in low nitrogen waters can only take up ammonium at maximal rates when supplies become available.

Ammonium is considered as the preferred nitrogen source for seagrasses (Moriarty and Boon 1989). Seagrass adsorb ammonium by their leaves, but they also pump nutrients from the sediment by their roots (McRoy and Barsdate 1970; McRoy and Goering 1974). The ammonium kinetics are still uncertain, as some authors found linear ammonia uptake by leaves with ammonia concentrations up to 20 $\mu mol\,l^{-1}$ (Iizumi and Hattori 1982) and some others described Michaelis-Menten kinetics with saturation occurring at ca 15 $\mu mol\,l^{-1}$ and above (Thursby and Harlin 1982). Our results indicate no saturation effect during the course of two hour enrichment experiments within a similar range of ammonium concentrations. Algae and seagrass ammonium affinity were of the same order of magnitude, whereas Corallinaceae uptake was lower in our experimental conditions.

We conclude that enrichment experiments can be used to evaluate nitrogen affinity of different benthic components of lagoon bottoms. Most of the affinity results from macrophytes, and to a lesser extent from microphytes. Previous studies have identified significant differences in benthic community structure of the SW New Caledonia lagoon (Chardy et al. 1988; Chardy and Clavier 1988a; Boucher and Clavier 1990). The three identified bottom types display significantly different physical, chemical and biological characteristics which would affect nutrient dynamics in the lagoon. The present results suggest that grey-sand bottoms (50% of the surface), which are the only community with a dense macrophyte cover, take up approximately 64.4% of available ammonium from the water column, whereas muddy bottoms (35% of the surface) and white-sand bottom (15% of the surface) consume 24.2 and 11.4% respectively. Grey-sand bottoms should thus approximately consume 2/3 of the ammonium circulating in the water column. It represents a major short-term nutrient sink in the New Caledonia lagoon system.

Acknowledgements. This research was supported by a French grant INSU/ORSTOM "AIP: Récifs Coralliens 90N50/0314". We thank the crew of ORSTOM R. V. Alis for the assistance at sea, S. Bonnet for chemical analyses, A. Di Matteo, P. Hamel, P. Laboute and J. Y. Panche for technical assistance. We also acknowledge the helpful comments of B. G. Hatcher and anonymous referees on the manuscript.

References

Andersen FO, Kristensen E (1988) The influence of macrofauna on estuarine benthic community metabolism: a microcosm study. Mar Biol 99:591–603

Atkinson MJ (1988) Are coral reefs nutrient limited? Proc 6th Int Coral Reef Symp 1:157–166

Bancroft KE, Paul EA, Wiebe MJ (1966) The extraction and measurement of adenosin-tri-phosphate from marine sediment. Limnol Oceanogr 21:473–479

Boto KG, Alongi DM, Nott ALJ (1989) Dissolved organic carbon-bacteria interactions at sediment water-interface in a tropical mangrove system. Mar Ecol Prog Ser 51:243–251

Boucher G, Boucher-Rodoni R (1988) In situ measurement of respiratory metabolism and nitrogen fluxes at the interface of oysterbeds. Mar Ecol Prog Ser 44:229–238

Boucher G, Clavier J (1990) Contribution of benthic biomass to overall metabolism in New Caledonia lagoon sediments. Mar Ecol Prog Ser 64:271–280

Button DK (1986) Affinity of organisms for substrate. Limnol Oceanogr 31:453–456

Capblancq J (1990) Nutrient dynamics and pelagic food web interactions in oligotrophic and eutrophic environments: an overview. Hydrobiologia 7:1–14

Chardy P, Clavier J (1988a) Biomass and trophic structure of the macrobenthos in the South-West lagoon of New Caledonia. Mar Biol 99:195–202

Chardy P, Clavier J (1988b) An attempt to estimate the carbon budget for the South West lagoon of New-Caledonia. Proc 6th Int Coral Reef Symp 2: 541–546

Chardy P, Chevillon C, Clavier J (1988) Major benthic communities of the south-west lagoon of New Caledonia. Coral Reefs 7:69–75

Charpy-Roubaud CJ (1986) Le microphytobenthos du lagoon de Tikehau (Polynésie Française). II. Production primaire. Notes Docums océanogr ORSTOM 28:51–80

Clavier J, Boucher G, Bonnet S, Di Matteo A, Gerard P, Laboute P (1990) Métabolisme aérobie du benthos et flux d'azote à l'interface eau-sédiment dans le lagon sud-ouest de Nouvelle Calédonie. Méthods et recueil de données. Rapp scient Tech ORSTOM Nouméa. Sci Mer, Biol Mar 54:1–35

Clavier J, Garrigue C, Boucher G, Bonnet S, Di Matteio A, Hamel P, Laboute P, Panche JY (1991) Flux d'oxygène et de sels nutritifs à l'interface eau-sédiment dans le lagon sud-ouest de Nouvelle-Calédonie: enrichissements en ammonium et action d'un inhibiteur de la photosynthèse. Méthode et recueil des données. Rapp scient Tech ORSTOM Nouméa, Sci Mer, Biol Mar 61:1–56

Corredor JE, Capone DG (1985) Studies of nitrogen diagenesis in coral reef sands. Proc 5th Int Coral Reef Congr 3:395–399

Crossland CJ (1983) Dissolved nutrients in coral reef waters. In: Barnes DJ (ed) Perspectives on coral reefs. AIMS, Clouston B Publisher, Australia, pp 56–68

D'Eila CF, DeBoer JA (1978) Nutritional studies of two red algae. II. Kinetics of ammonium and nitrate uptake. J Phycol 14: 266–272

DeBoer JA (1981) Chapter 10: Nutrients. In: Lobban CS, Wynne MJ (eds) The biology of seaweeds. (17 Botanical Monographs) Blackwell, pp 356–392

Dodds WK, Priscu JC (1990) Development and application of a technique for estimating nutrient deficiency in soft sediments. Hydrobiologia 203:93–97

Garrigue C, Di Matteo A (1990) La biomasse végétale benthique du lagon sud-ouest de Nouvelle-Calédonie. Résultats bruts: listes taxonomiques, biomasses, pigments chlorophylliens. Arch Sci Mer Noumea ORSTOM Biol Mar 1:1–143

Goldman JC, Glibert PM (1982) Comparative rapid ammonium uptake by four species of marine phytoplankton. Limnol Oceanogr 27:814–827

Grigg RW, Polovina JJ, Atkinson MJ (1984) Model of a coral reef ecosystem. III. Resource limitation, community regulation, fisheries yield and resource managment. Coral Reefs 3:23–27

Haines KC, Wheeler PA (1978) Ammonium and nitrate uptake of the seaweeds *Hypnea musicformis* (Rhodophyta) and *Macrocystis pyrifera* (Phaeophyta). J Phycol 14:319–332

Hanisak MD, Harlin MM (1978) Uptake of inorganic nitrogen by *Codium fragile* ssp. *tomentosoides* (Chlorophyta). J Phycol 14: 450–454

Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of epilithic algal community on a coral reef. J Exp Mar Biol Ecol 69:61–84

Höpner T, Wonnenberger K (1985) Examination of the connexion between the patchiness of benthic nutrient efflux and epiphytobenthos patchiness on intertidal flats. Netherl J Sea Res 19: 277–285

Iizumi HA, Hattori A (1982) Growth and organic production of eelgrass (*Zostera marina*) in temperate waters of the Pacific coast of Japan. III. The kinetics of nitrogen uptake. Aquat Bot 12:245–256

Johnstone R, Koop K, Larkum AWD (1989) Fluxes of inorganic nitrogen between sediments and water in a coral reef lagoon. Proc Linn Soc N S W 110:219–227

Kinsey DW (1985) The functional role of back-reef and lagoonal systems in the central Great Barrier Reef. Proc 5th Coral Reef Congr Tahiti 6:223–228

Kinsey DW, Domm A (1974) Effects of fertilization on a coral reef environment. Primary production studies. Proc 2nd Int Coral Reef Symp 1:49–66

Larkum AWD (1983) The primary productivity of plant communities on coral reefs. In: Barnes DJ (ed) Perspectives on coral reefs. AIMS, Clouston B Publisher, Australia, pp 221–230

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnol Oceanogr 12: 343–346

Mackin JE, Aller RC (1984) Ammonium adsorption in marine sediments. Limnol Oceanogr 29:250–257

McRoy CP, Barsdate RJ (1970) Phosphate absorption in eelgrass. Limnol Oceanogr 15:6–13

McRoy CP, Goering JJ (1974) Nutrient transfert between the seagrass *Zostera marina* and its epiphytes. Nature 248:173–174

Moriarty DJW, Boom RJ (1989) Interactions of seagrasses with sediment and water. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses, Aquatic Plant Studies 2. Elsevier, Amsterdam, New York, pp 500–535

Priscu JC, Priscu LR (1984) Inorganic nitrogen uptake in oligotrophic lake Taupo, New Zealand. Can J Fish Aquat Sci 41: 1436–1445

Raven JA (1976) Transport in algal cells. In: Lüttge U, Pitman MG (eds) Transport in plants IIA, Encyclopedia of plant physiology. Springer Verlag, New York Heidelberg Berlin, pp 129–188

Rosenfeld JK (1979) Ammonium adsorption in nearshore anoxic sediments. Limnol Oceanogr 24:356–364

Rougerie F, Wauthy B (1986) Le concept d'endo-upwelling dans le fonctionnement des atolls-oasis. Oceanol Acta 9:133–148

Siegel S (1956) Non parametric statistics for the behavioral sciences. McGraw-Hill, New York, p 312

Sokal RR, Rohlf FJ (1981) Biometry. Freeman and company, New York, p 859

Solorzano L (1969) Determination of ammonia in natural waters by phenylhypochlorite method. Limnol Oceanogr 14:799–801

Stanley SO, Boto KG, Alongi DM, Gillian FT (1987) Composition and bacterial utilization of free-amino acids in tropical mangrove sediments. Mar Chem 22:13–30

Sundbäck K, Granéli W (1988) Influence of microphytobenthos on the nutrient flux between sediment and water: a laboratory study. Mar Ecol Prog Ser 43:63–69

Thursby GB, Harlin MM (1982) Leaf-root interactions in the uptake of ammonia by *Zostera marina*. Mar Biol 72:409–412

Van Es FB (1982) Community metabolism of intertidal flats in the Ems-Dollard estuary. Mar Biol 66:95–108

Wiebe WJ, Johannes RE, Webb KL (1975) Nitrogen fixation in a coral reef community. Science 188:257–259

Williams SL, Yarish SM, Gill IP (1985) Ammonium distribution, production, and efflux from backreef, St. Croix, US Virgin. Mar Ecol Prog Ser 24:57–64