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Cycling of phosphorus maintains the production of microphytobenthic communities in carbonate sediments of a coral reef

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Abstract

The phosphorus (P) cycle that maintains the production of microphytobenthic communities in carbonate sediments was investigated in the fringing Shiraho coral reef system located off the east coast of Ishigaki Island, Japan. Production rates of the diatom-dominated microphytobenthic communities and the P flux at the sediment–water interface were determined by in situ benthic enclosure experiments. The daily net production (6.9–24 mmol C m^{-2} d^{-1}) by microphytobenthic communities in carbonate sediments accounted for 14–27% of organic carbon excess production by the bulk reef communities. Despite the observed active photosynthesis, the exchange of P across the sediment–water interface was negligible. This implies that P in seawater is a minor source for the production of microphytobenthic communities. In situ bottle incubation experiments also demonstrated that P in seawater is a minor source and that P adsorbed on sediment particles is the significant source for production. Laboratory experiments led to an estimated concentration of adsorbed P in the carbonate sediments of ~0.39 μmol P g^{-1} dry wt, which corresponds to 5.5% of total P. This source can be rapidly released into seawater as dissolved reactive P, the most available P form. Thus, high primary productivity rates of the microphytobenthic communities is largely maintained by this sedimentary pool of P. Furthermore, the communities play an important role in retaining P in the carbonate sediments through uptake at the sediment–water interface before it can diffuse away.

Carbonate sediments containing coral fragments and coralline algal skeletons occupy a significant area in many coral reefs. Microphytobenthic communities in carbonate sediments are able to maintain high primary productivity rates in relatively low-nutrient seawater (e.g., Boucher et al. 1998; Uthicke and Klumpp 1998). This apparent paradox has led to many studies seeking to identify and quantify sources and cycling of nutrients that maintain benthic productivity in the carbonate sediments of coral reefs. Sediment feeders such as holothurians play an important role in supplying ammonia as a nitrogen source for benthic production (Uthicke and Klumpp 1998). Nitrogen (N) fixation has been suggested as a major source of nutrient N in reef sediments (Capone et al. 1992; Miyajima et al. 2001). Thus, in the oligotrophic ecosystems of reef carbonate sediments, where N fixation potentially supports the N requirement, phosphorus (P) should be a limiting nutrient for primary production. A supply of P for maintaining microphytobenthic production can-

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not be generated in situ like fixed N. Although it is important to identify sources and cycling of P, there have been few investigations of P metabolism by microphytobenthic communities in carbonate sediments.

It has been shown that the exchange of P between seawater and benthic communities is surprisingly small in comparison to the flux of P across reef flats in many coral reefs (Pilson and Betzer 1973; Johannes et al. 1984; Atkinson 1987; Charpy-Roubaud et al. 1990). These observations support suggestions that P in the overlying seawater is a minor source for benthic production and that a large proportion of P requirements for production are tightly supplied by remineralization and recycling processes. Remineralization of P may occur largely at the sediment–water interface (SWI), within the sediments, or in both places. The importance of P recycling at the SWI and within the sediments can be examined by measuring P flux across the SWI. Diffusional fluxes of nutrients from carbonate sediments have been estimated based on concentration measurements of gradients in pore water (Charpy-Roubaud et al. 1996), direct measurements using in situ benthic enclosures (Williams et al. 1985; Boucher and Clavier 1990), and laboratory intact core experiments (Miyajima et al. 2001). Desorption of P from sediment particles is also supposed as an important pathway supplying P from carbonate sediments (Entsch et al. 1983). However, little information currently exists to evaluate the availability of potential P sources from carbonate sediments for the P requirements by the microphytobenthic production.

This study has focused on the role of P cycling in maintaining microphytobenthic primary production in carbonate sediments in the coral reef ecosystem of Shiraho Reef off Ishigaki Island, Japan. Shiraho Reef was demonstrated to have remarkably high organic productivity (Kayanne et al. 1995). An important issue to identify is the relative contribution of various communities, including the microphytobenthos, in reef production in order to understand the mechanism of the high productivity of coral reefs in oligotrophic environments. Although N cycling in the benthic systems of Shiraho Reef has been extensively investigated by Miyajima et al. (2001), the source and cycling of P that maintain high productivity are unknown. Field observations, in situ incubations, and laboratory experiments were carried out to examine the importance of microphytobenthic communities in the reef productivity and to identify P cycling in the carbonate sediments of the reef.

Materials and methods

Study area—This study was conducted at Shiraho Reef located off the east coast of Ishigaki Island in the western subtropical Pacific (24°25′N, 124°20′E; Nakamori et al. 1992). Shiraho is a fringing coral reef with a reef crest at ca. 850 m off the shoreline and a reef flat (up to 3 m below mean sea level) inside (Fig. 1). Typical beltlike zonated vegetation is observed in the reef flat. Seagrass beds are observed up to ca. 200 m off the shoreline. Large patches of live corals are found abundantly at 500–700 m off the shoreline. The backward area of the reef crest (700–800 m off) is covered with dense brown algal vegetation from spring to

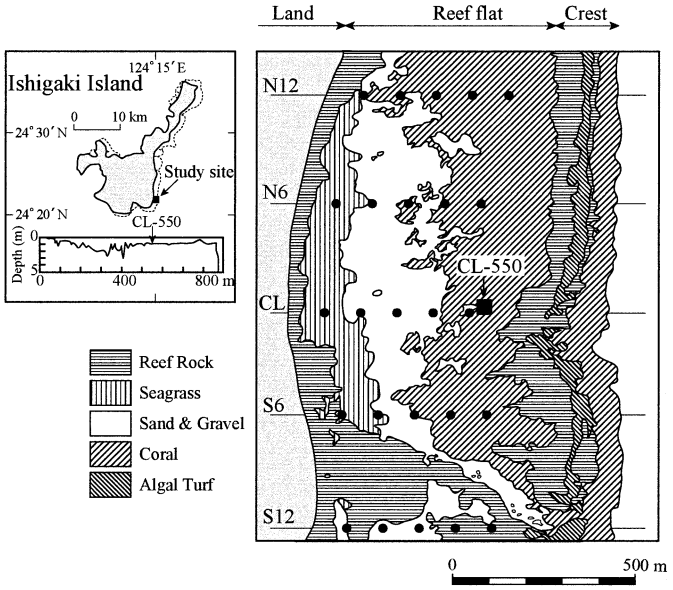

Fig. 1. Map of the observation area in Shiraho Reef. The distribution of organisms is adapted from Nakamori et al. (1992). The symbols (circle) show the sediment sampling location for C and P analyses.

autumn (mainly *Sargassum* spp. and *Padina* spp.). Most of the other areas of the reef flat are devoid of macrophytes or corals and are composed of typical carbonate sediments formed from coral fragments and skeletons of coralline algae. The area covered with carbonate sediments is ca. 0.3 km^2, accounting for 30% of the total reef area.

Chemical analyses of carbonate sediments—Chlorophyll *a* (Chl *a*) concentrations in surface carbonate sediments were measured to investigate the spatial distribution of microphytobenthic biomass in the reef flat. In September 1997, 16 locations (200–550 m off the shore at 50-m intervals) were sampled along Transects CL and S6 (Fig. 1). Surface sediments (0–1 cm) were collected by divers using a plastic syringe (2 cm i.d.) as a corer. Duplicate samples were collected at each sampling site totaling 32 samples. At station CL-550 (550 m off the shore on Transect CL, Fig. 1), the surface Chl *a* concentration also was monitored in March and September 1998 and March 1999 to investigate temporal variation of microphytobenthic biomass. In the September 1998 observation, three replicate cores were collected to investigate vertical profiles of Chl *a* in the sediments. The core samples were sliced into 1-cm-thick sections and extracted for Chl *a* analyses. Remaining portions of the sliced subsamples were used for elemental analyses of P and C as described below. Concentration of Chl *a* in sediment samples was determined spectrophotometrically by *N*,*N*′-dimethylformamide (DMF) extraction (Suzuki et al. 1993). Extraction was carried out by mixing 10 g (wet wt) of the sample and 10 ml of DMF. The mixture was stored at −20°C for 12 h to complete extraction. Particulate materials were then removed by centrifugation at −20°C and 4,000 rpm (3,300 × g) for 10 min. The optical density of the extract was measured at 663.8, 646.8, and 750 nm to estimate the Chl *a*

concentration using the extinction coefficient method (Porra et al. 1989). Portions of the DMF extracts were subjected to photosynthetic pigment analysis using high-performance liquid chromatography (HPLC, Oku and Kamatani 1999). The HPLC apparatus (Hitachi L-6000) was fit with a C-18 column (Merck LiChrosphere RP-18-5, 4.6 mm i.d., 150 mm long, 5 μm particle size). The pigments were eluted successively with methanol–0.5 M ammonium acetate buffer (80 : 20, v/v), methanol–0.5 M ammonium acetate buffer (90 : 10, v/v), methanol–acetone (90 : 10), and methanol–acetone (60 : 40). Each pigment was detected at 436 nm and 660 nm using a Shimadzu SPD-10A-vp spectrometer. Identification of the major pigments was based on the adsorption spectra (360–750 nm) of each peak.

Concentrations of total, inorganic, and organic P and organic C were determined in surface sediments from 25 locations (100–500 m offshore) along each observation transect (Fig. 1) at 100-m intervals. Vertical profiles of P and C were also investigated using the remaining portions of the sliced sediment samples used in Chl *a* analysis described above. The samples were freeze-dried and ground. P concentrations were determined by the method of Aspila et al. (1976). Briefly, inorganic P was measured after dilute HCl extraction followed by dissolved reactive phosphate (DRP) analysis of the acid extract. To determine total P, the sediment samples were combusted at high temperature (500°C for 2 h), extracted with HCl, and analyzed for DRP. Organic P concentration was estimated as the difference between total and inorganic P. Organic C was determined using a Yanaco CN analyzer after acid vapor treatment to remove carbonates (Yamamuro and Kayanne 1995).

Pore-water profiles of DRP were investigated in duplicate sediment cores collected at station CL-550 (Fig. 1) in March and September 1998. According to the protocol by Miyajima et al. (2001), pore water was extracted from the sliced subsamples at depth intervals of 2.5–3.0 cm. DRP was measured using a Technicon Autoanalyzer II using the standard method of Strickland and Parsons (1972). DRP was analyzed with detection limits of ~0.01 μM and with the typical reproducibility of $\pm$0.01 μM.

Microscopic observation of microphytobenthos—Species of microphytobenthic organisms in carbonate sediments were identified and enumerated by microscopic observation. Portions (20 ml) of sediment samples from sediment core depths of 0–1, 3–4, and 8–9 cm collected at station CL-550 in September 1998 were used. The samples were mixed with 30 ml of seawater filtered with a Whatman GF/F glass fiber filter, which contained 2% formaldehyde, and stored at 5°C until analysis. To recover algal cells from sediment, the mixtures were vigorously blended and then allowed to sit for sedimentation of sand particles. A portion of the resulting suspension was utilized for microscopic observation.

An experimental biscuit plate was employed to collect species that may be difficult to recover from the sediment particles because of their fragility and adhesiveness. The plate (9.8 $\times$ 9.8 $\times$ 0.5 cm) was placed on the bottom of station CL-550 for 25 d in September 1998. Then, the attached organisms were gently stripped off using a spatula into filtered seawater containing 2% formaldehyde. The suspension was stored at 5°C and observed microscopically.

In situ incubation experiments—Benthic community production and P flux at the SWI were investigated by in situ incubation experiments. Benthic enclosures were installed at station CL-550 in the late winter season of March 1998 and 1999 and in the late summer season of September 1998. Information on the duration and timing of the incubation is given in Table 2. Water depth at the station varied with tide and ranged from 1.3 to 2.3 m during the experiments. Barrel-shaped clear acrylic and shaded PVC chambers, with a circular area of 280 cm^2 and a volume of 5 L, were used for light and dark treatments, respectively. These experiments were carried out in triplicate. The chamber was equipped with an impeller, a sampling port with a stopcock, and a plastic bag that compensates for water removed during sampling. After appropriate incubation times, the water samples were withdrawn from the sampling port by divers using glass syringes. The samples were poured into 50 ml bottles for determination of dissolved oxygen (DO) by Winkler's method (Grasshoff 1983). For DRP analyses, 10-ml portions of samples were filtered thorough GF/F filters and stored in acrylic tubes at $-$20°C until analysis. Total changes in DO and nutrient concentrations in the chambers (sediment and water) were corrected for changes in the bottles containing seawater alone. During the day of the enclosure experiment, water temperature and light intensity (as photosynthetically available radiation, PAR) were monitored with a seawater sensor (H20 sensor, HYDROLAB) and an underwater quantum sensor (LI-192SA, Li-Cor), respectively. The sensors were connected to an integrated monitoring system, and the data were logged every 1 min.

In situ bottle incubation experiments were executed concurrently with the enclosure experiment of March 1998. A 400-g portion of sediment sample (0–2 cm) from station CL-550 was washed gently by soaking with 4 liters of the seawater filtered with a GF/F filter. The washed sediment was retrieved on a stainless sieve (200 μm mesh), and large particles (greater than ~5 mm) were manually removed. The sample was divided equally between glass bottles (Duran® 300 ml, ~10 g wet wt sand per bottle). The bottles were gently filled with the filtered seawater containing 0.03 μM of DRP and capped tightly without any bubbles. P-enriched treatment was prepared by the addition of DRP (as potassium dihydrogen phosphate) at a concentration of 3 μM. Killed control treatments were prepared by the addition of mercury chloride to a concentration of 0.2%. Triplicate bottles for each treatment were placed on the bottom at station CL-550 for 4 h daytime (ca. 1150–1605 h). The thickness of the sediment in the bottle was ~3 mm. After incubation, the seawater in the bottle was sampled for DO and DRP measurements in the same manner as the benthic enclosure experiment.

Laboratory experiments for DRP release from carbonate sediment—Two types of laboratory experiments were conducted to obtain further information on the nature and extent of P cycling in the carbonate sediments. A portion of surface sediment sample (0–2 cm) used in the above bottle incu-

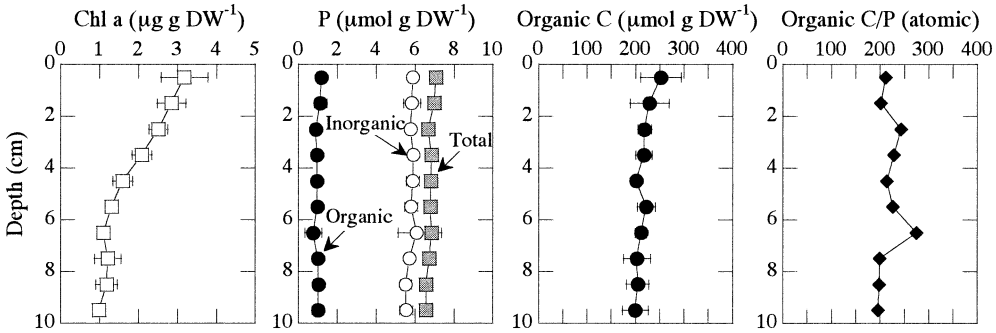

Fig. 2. Vertical profiles of the concentrations of Chl *a*, three forms of P, organic C, and organic C/P ratio in sediment collected at station CL-550 in September 1998.

bation experiments was used in the laboratory experiments. The sample was divided into 16 glass vials (1.5 g wet wt per vial), and a 10-ml portion of the filtered seawater containing 0.03 μM DRP was added with mercury chloride (0.2%) to inhibit microbial activities. The vials were shaken continuously at 25 ± 1°C, which is equivalent to the ambient water temperature during the in situ bottle incubation experiment. The solution phase was recovered from two vials at intervals by settling for 1 min and filtration (GF/F filter) and then analyzed for DRP. In the second experiment, two vials were prepared in the same manner as above. After 24 h equilibration, the solution phase was removed by filtration and analyzed for DRP. This procedure was repeated with additions of 10 ml of seawater.

Results

Concentration of Chl a *and identification of microphytobenthos in carbonate sediments*—The average concentration of Chl *a* in the surface sediment samples from 16 locations was 3.4 ± 0.9 μg Chl *a* g^{-1} dry wt (mean ± 1 SD, n = 32). No considerable trend was found in the spatial distribution, indicating that microphytobenthos homogeneously inhabit the reef flat area. Chl *a* concentration in the surface sediment at station CL-550 was 3.7 and 3.2 μg Chl *a* g^{-1} dry wt in the late summer season (September 1997 and 1998, respectively) and 3.7 and 2.8 μg Chl *a* g^{-1} dry wt in the late winter season (March 1998 and 1999, respectively). Considering the errors in triplicate sample measurements, seasonal variation of Chl *a* concentration was negligible (ANOVA, P = 0.29). Figure 2 shows the vertical profile of Chl *a* concentration in the sediment at station CL-550. The concentration decreased within the top 6 cm of sediment and reached about half of the surface value. Below this zone, the concentration was relatively constant around 1.1–1.5 μg Chl *a* g^{-1} dry wt. Without acidification, the measurement of Chl *a* probably overestimates the concentration because of absorbance of phaeophytin. That would explain the constant concentrations observed below 6 cm. The results of HPLC analysis, however, demonstrated the absence of phaeophytin in the sediments below 6 cm.

The HPLC analysis identified 11 peaks of photosynthetic pigments in the DMF extracts from sediment samples. The most abundant pigment was Chl *a* followed by fucoxanthin and Chl *c*, suggesting that sediments had an enriched population of Bacillariophyta (diatoms) according to Hoek et al. (1995). The presence of zeaxanthin and the absence of Chl *b* observed in the pigment analysis indicate the occurrence of Cyanophyta. In microscopic observation of the sediment sample, diatoms were dominant, particularly representatives of the genera *Amphora, Nitzschia,* and *Navicula.* Uthicke (1999) also observed dominance of diatoms (*Navicula* spp. and *Amphora* spp.) in sediments of the Great Barrier Reef. Although the occurrence of Cyanophyta has been speculated from the results of HPLC pigment analyses and from the N fixation activity observed in the carbonate sediments of the study area (Miyajima et al. 2001), no direct evidence was provided by microscopic observation of the sediment samples. On the other hand, Cyanophyta (e.g., *Lyngbya*) were identified in the sample recovered from the experimental plate. A small abundance of Chlorophyta was also identified only in the plate sample. Fragility and adhesiveness of Cyanophyta and Chlorophyta in comparison with diatoms presumably hampered the recovery of these species from the sediment particles.

Concentrations of phosphorus and carbon in carbonate sediments—Concentrations of three forms of P and organic C in the surface sediment samples were compiled in Table 1. The mean concentration of total P was 7.49 ± 0.58 μmol P g^{-1} dry wt in the surface sediments collected at 25 locations in the reef flat. This value was consistent with those reported in carbonate sediments of various coastal seas (Entsch et al. 1983; Szmant and Forrester 1996; Jensen et al. 1998). Higher concentrations were found in the samples from nearshore locations (100 m offshore), indicating a terrestrial influence on the sediment. The results of phosphorus fractionation revealed that inorganic P was the dominant form of sediment P pools, accounting for 85–87% of total P. The mean organic C concentration (0.21 mmol C g^{-1} dry wt) also was consistent with those in other coastal carbonate sediments (Erftemeijer et al. 1994). Figure 2 shows the vertical profiles of concentrations of P and organic C in the sediment at station CL-550. Although the concentration of Chl *a* exhibited a considerable decrease in the upper layers with depth, homogeneous distributions were observed in P and C concentrations from the surface to 10 cm depth.

The pore-water DRP profiles showed significant concen-

Table. 1. Concentrations of total, inorganic, and organic P and organic C in samples of surface carbonate sediments, growing corals, and coralline algae in Shiraho Reef.

Sample	Total P (μmol g^{-1} dry wt)		Inorganic P (μmol g^{-1} dry wt)		Organic P (μmol g^{-1} dry wt)		Organic C (mmol g^{-1} dry wt)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Carbonate sediment (n = 25)	7.49	0.58	6.49	0.52	1.00	0.15	0.21	0.03
100 m offshore (n = 5)	8.25	0.37	7.20	0.37	1.05	0.11	0.23	0.03
200 m offshore (n = 5)	7.45	0.39	6.35	0.27	1.10	0.15	0.19	0.02
300 m offshore (n = 5)	7.57	0.51	6.58	0.53	0.99	0.13	0.22	0.04
400 m offshore (n = 5)	7.04	0.25	6.12	0.29	0.92	0.11	0.17	0.02
500 m offshore (n = 5)	7.12	0.41	6.18	0.30	0.95	0.22	0.21	0.02
Growing coral (n = 42)	5.53	1.79	1.46	1.07	4.07	1.39	1.14	0.48
Porites (n = 14)	5.56	1.35	1.21	0.35	4.35	1.40	1.25	0.31
Montipora (n = 7)	7.89	1.96	3.55	0.81	4.34	2.04	1.85	0.36
Heliopora (n = 7)	3.90	1.28	0.64	0.30	3.27	1.04	1.07	0.37
Acropora (n = 7)	5.24	1.33	1.37	0.25	3.87	1.39	0.71	0.23
Pavona (n = 7)	5.05	0.82	0.79	0.36	4.25	0.82	0.72	0.12
Coralline algae (n = 17)	13.1	5.42	5.65	2.35	7.48	5.75	11.7	5.52
Padina sp. (n = 7)	17.9	4.10	4.27	1.58	13.6	3.38	16.7	2.80
Galaxaura sp. (n = 6)	11.5	2.85	7.72	2.42	3.82	0.67	11.0	2.10
Jania sp. (n = 4)	7.24	2.37	4.97	0.97	2.26	1.55	3.95	1.01

tration gradients with depth (Fig. 3). Maximum gradients were observed at the SWI, especially in the March samples, in which the concentration reached a constant value (~2 μM) just below the SWI. On the other hand, the surface concentration gradient was relatively small in the September samples, and the concentration gradually increased with depth to the level comparable to that in the March samples at around 15 cm depth. The presence of considerable concentration gradients at the SWI suggests active diffusional DRP flux from the sediments to the overlying seawater.

Carbon production of microphytobenthic communities—Carbon production rates of microphytobenthic communities measured by benthic enclosures are compiled in Table 2. In this study, carbon production was indirectly calculated from O_2 production data with net photosynthetic quotient (PQ) and community respiratory quotient (RQ). It has been reported that the quotients vary among sites and seasons in some coral reef benthic communities (PQ = RQ^{-1} = 1.0–1.1, Atkinson and Grigg 1984; Barnes and Devereux 1984). Other estimates, however, have suggested that typical coral reef flats have community metabolic quotients close to 1.0 (Smith and Marsh 1973; Barnes 1983). In the absence of better estimates, it is reasonable to assign a value of 1.0 (1 mg O_2 = 31.3 μmol C) to both metabolic quotients. Net production and respiration rates were estimated from light- and dark-chamber experiments, respectively. Gross photosynthetic rates were calculated as the sum of these productions. The results show that benthic community production rates varied considerably with a wide range among each experiment (Table 2). Because seasonal variations of surface Chl *a* concentrations were negligible (*see above*), the large variations in these metabolic rates should result from changes in ambient conditions such as irradiance, water temperature, and nutrient status.

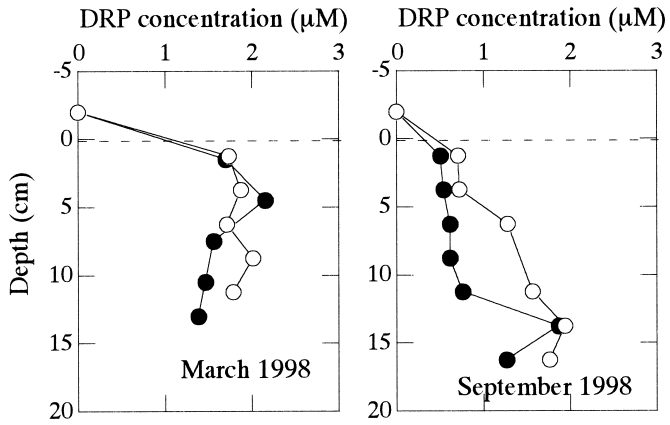

Fig. 3. Pore-water profiles of DRP concentration at station CL-550. Open and solid symbols express DRP concentrations from duplicate core samples, respectively.

Using the photosynthesis rate and integrated irradiance data obtained from the experiments (Table 2), an area-specific value for photosynthetic efficiency or amount of carbon fixed per amount of quanta, can be presented. This value theoretically can reach a maximum of 125 mmol C [mol E]$^{-1}$. We found that the value ranged from 1.0 to 1.8 with an average value of 1.4 mmol C [mol E]$^{-1}$. A similar low efficiency of 4.2 mmol C [mol E]$^{-1}$ was measured in microphytobenthic communities in carbonate sediments of the Great Barrier Reef (Uthicke and Klumpp 1998). The daily photosynthetic production was then calculated with the area-specific efficiency and integrated irradiation during the daytime. The daily respiration rate was calculated assuming a constant rate of respiration over a 24-h period. The calculated daily net production values are shown in Table 2, ranging from 6.9 to 23.5 mmol C m^{-2} d^{-1}.

Table 2. Experimental conditions, metabolic rates (mmol C m^{-2} h^{-1}) of microphytobenthic communities, and DRP flux (μmol P m^{-2} h^{-1}) at the sediment–water interface during the benthic enclosure experiments.

Date of experiment	Incubation period	Mean water temperature	Mean irradiance* (μmol E m^{-2} s^{-1})	Respiration	Gross photo-synthesis	Net production†	DRP flux‡	
							Light	Dark
9 Mar 1998	930–1400 h	25.0°C	1,129 (18.3 mol E m^{-2})	0.71±0.2	5.8±0.2	5.1±0.2 (23.5±1.3)	−1.5±0.21	0.67±0.09§
21 Sep 1998	930–1800 h	29.5°C	63 (19.0 mol E m^{-2})	1.3±0.1	4.0±0.3	2.7±0.3 (6.9±3.9)	−0.86±0.13	0.49±0.10§
18 Mar 1999	850–1800 h	23.8°C	626 (20.7 mol E m^{-2})	0.25±0.1	2.3±0.4	2.0±0.4 (14.8±5.2)	−0.27±0.06§	0.20±0.02§

* The values in parentheses show integrated irradiance during the experiments.
† The values in parentheses show daily net production rate (mmol C m^{-2} d^{-1}).
‡ Positive and negative values for DRP flux indicate release from and uptake into sediment, respectively.
§ These values were based on insignificant change in DRP concentrations at the detection limit of analysis.

Phosphorus exchange between sediment and seawater—Table 2 shows the rates of DRP exchange across the SWI, which were estimated as the changes in DRP concentrations in the seawater enclosed by the chambers during incubation. Despite the observed high production rate of microphytobenthic communities, the flux of DRP across the SWI was negligible; the changes in DRP concentrations were around the minimum detection limit of the analytical method used. Figure 4 shows the results of the in situ bottle incubation experiments. As observed in the enclosure experiments, no significant change in DRP concentration was observed in the control bottles, despite active photosynthetic production. The addition of the mercury chloride inhibitor seemed to completely inhibit microbial activities because DO concentrations were found to be constant in the killed-control bottles during incubation (Fig. 4). Considerable increases (2.13 ± 0.05 μM) and decreases (2.30 ± 0.06 μM) in DRP concentrations were observed in the killed-control and P-enriched treatments, respectively. In the killed-control treatment, because of inhibition of biological activities, the DRP increase could have resulted from chemical reactions (e.g., desorption from sediment particles). Utilization through active photosynthesis should be responsible for the decrease in DRP concentration in the P-enriched treatment. The rates of P desorption and utilization in these treatments were estimated to be approximately the same value at 0.23 and 0.21 μmol P g^{-1} dry wt h^{-1}, respectively. The similarities in the rates of desorption and utilization likely led to no apparent change in the DRP concentration in the control.

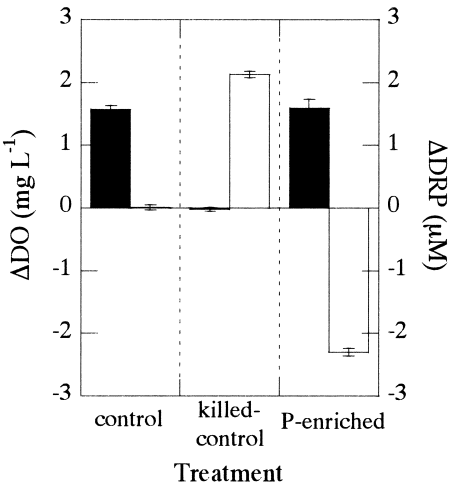

Fig. 4. Changes in concentrations of DO (mean ± SD, filled bars) and DRP (mean ± SD, open bars) in the in situ incubated bottles. The initial concentration of DO was 6.06 mg L^{-1}, and those of DRP were 0.05 and 2.94 μM in the control and P-enriched treatments, respectively.

Figure 5A shows the results of the laboratory experiment, where DRP release from the carbonate sediment is illustrated as a function of time. DRP was rapidly released from the sediment during the initial 10 min. Within 10 h of the start of experiment, DRP concentrations reached maximum and constant values of 3.9 μM, which was almost twice the DRP concentration in the ambient pore waters (Fig. 3). The maximum release rates were found to be 12.4 μM h^{-1} and were achieved during the initial 2 min (Fig. 5A). Figure 5B shows the results of the repeated 24-h desorption equilibrium experiments. The equilibrium concentration of DRP in seawater decreased with repetition. However, a considerable concentration of DRP (0.68 μM) was found even after seven repetitions of the equilibrium experiments.

Discussion

Biomass and productivity of microphytobenthic communities in carbonate sediments—The results of measurement of Chl *a* concentrations revealed that microphytobenthic organisms were widely distributed in the reef flat of Shiraho Reef. The concentration of Chl *a* measured here represents the total biomass in the bulk sediment of the sampled layer (0–1 cm). It is more important to accurately estimate biomass in the photic zone of the sediment in order to obtain accurate productivity measurements. We employed two options to estimate productive biomass in carbonate sediments. First, using data from the bottle incubation experiments, the biomass-specific photosynthesis rate was calculated to be 140 μmol C [mg Chl *a*]$^{-1}$ h^{-1} using the photosynthesis rate measurements and the Chl *a* concentrations in the sediments. Applying this value to the photosynthesis rate (5.1 mmol C

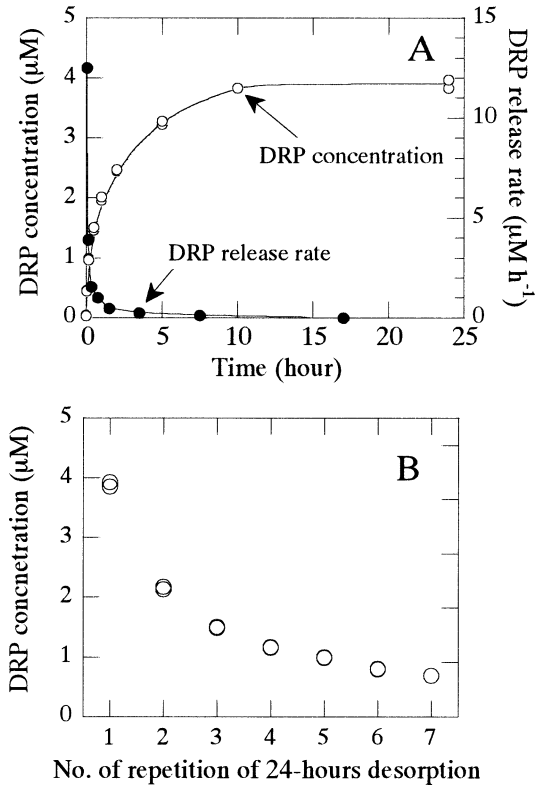

Fig. 5. Release of DRP from carbonate sediment. (A) The DRP concentration in seawater (open circle) and the rate of DRP release from sediment (solid circle) as a function of time. (B) The concentration of DRP in seawater after each repetition of 24-h equilibrium with the sediment.

m^{-2} h^{-1}) measured in the concurrent benthic enclosure experiments (March 1998, Table 2), the standing stock of Chl *a* attributed to primary production was then estimated as 36.4 mg Chl *a* m^{-2}. However, because the sediment samples used in the bottle incubation had been washed and sorted by size before experiments, such pretreatments were likely to introduce a bias in this estimate. The second estimate for productive biomass is based on published estimates of the depth of photic zone. Using fiber optic microprobes, the depth of the photic zone in sandy marine sediments was estimated to reach 4 mm in depth (Kühl and Jørgensen 1994; Kühl et al. 1994; Taylor and Allison 1999). The productive biomass in the photic zone is then calculated to range from 15.0 to 19.9 mg Chl *a* m^{-2} using the mean concentration of Chl *a* in the 0–1 cm layer. Because the Chl *a* concentrations decreased rapidly with depth within a few centimeters of the surface sediment (Fig. 2), it is possible that using the mean concentration in the 0–1-cm layer underestimated the biomass in the top 4 mm. There is a large variation of the productive biomass among each estimation method (15.0–36.4 mg Chl *a* m^{-2}), and the values could involve biases due to the limitations in experimental manipulations. However, the productive biomass in the carbonate sediment is considerably important in the reef ecosystems; the values are two orders of magnitude higher than that in the seawater column of the study area at a mean water depth of 2 m (~0.32 mg Chl *a* m^{-2}, Yamamuro and Kayanne 1997). The estimate of the productive Chl *a* gives a mean chlorophyll-specific productivity of 172 μmol C [mg Chl *a*]$^{-1}$ h^{-1}. The maximum value of 290 μmol C [mg Chl *a*]$^{-1}$ h^{-1} obtained in the experiment of March 1998 is higher than values reported by Pinckney and Zingmark (1993) for a very productive coastal mudflat, where the highest rates were 70–220 μmol O_2 [mg Chl *a*]$^{-1}$ h^{-1}. This suggests that microphytobenthic communities in carbonate sediments exhibit a relative high efficiency of photosynthesis, which is likely responsible for high productivity of the coral reef ecosystems.

In this study, the daily net production (6.9–23.5 mmol C m^{-2} d^{-1}, Table 2) was estimated by multiplying the mean value of the area-specific efficiency of photosynthesis during incubation by integrated irradiance during the daytime. However, because previous studies revealed that the relationship between photosynthetic efficiency (a biomass-specific value, Ψ) and irradiance is nonlinear (Pinkney and Zingmark 1993; MacIntyre et al. 1996), our estimates likely involve some errors. The values reported here could be compared to those estimated by more precise measurements of net production rates of microphytobenthic communities in other carbonate sediments. Precise measurements have been accomplished in various coral reefs using data-logging respirometers and in situ irradiance monitoring, which allowed the construction of production–irradiance (*P–I*) curves (e.g., Boucher et al. 1998; Uthicke and Klumpp 1998). A comparison of daily net production of microphytobenthic communities from this study with these previously published studies shows that our value is consistent with those from other reefs. Most of the presented data have suggested net accumulation of organic matter through microphytobenthos production.

The importance of microphytobenthic communities in the carbonate sediments could be evaluated by comparing their production with that of bulk communities in the coral reef. On the days of the enclosure experiments of September 1998 and March 1999, the bulk community production of the reef was concurrently measured using an in situ continuous monitoring system of dissolved inorganic carbon, total alkalinity, and DO in the reef water at station CL-550 (Kayanne et al. unpubl. data). It was estimated that the net production by the microphytobenthos accounted for 27.0 and 13.7% of that by the bulk reef communities in September 1998 and March 1999, respectively. This is consistent with the results of Boucher et al. (1998), who estimated that soft bottom production accounts for 2.8–32% of the bulk community production of a barrier reef flat in Moorea, French Polynesia. These results infer that microphytobenthos is one of the significant primary producers in the coral reef ecosystems.

Source of phosphorus for microphytobenthos production—The high productivity of the microphytobenthic communities observed in the enclosure and bottle incubation experiments suggested the presence of P sources enough to account for production. The overlying seawater contained a very low concentration of DRP, and the exchange of DRP across the SWI was negligible (Table 2). This strongly indicates that photosynthetic production by the microphytobenthic communities mainly utilized sedimentary pools of P, but not DRP in the overlying seawater. Some possible sourc-

es and pathways that support photosynthetic productivity in carbonate sediments include (1) DRP in pore water, (2) diffusional flux of DRP from the deeper layer of sediments to the surface photic zone, and (3) bioturbation of sediments, excretion of nutrients by macrobenthic organisms, or both. The sediment pore waters contained much higher concentrations of DRP (0.5–2 μM) than the overlying seawater. The standing stock of pore-water DRP could be estimated from the DRP concentration and water content of the sediments. The amount of pore-water DRP was then calculated as ~3 μmol P m^{-2} in the top 1 cm of sediments. Diffusional flux from the deeper layer of sediments to the surface photic zone can be estimated using concentration gradients of DRP in pore water. Unfortunately, our method to determine the pore-water DRP profiles could not provide a precise concentration gradient. Based on the precise measurements of pore-water DRP, previous studies have estimated DRP diffusional flux from carbonate sediments to seawater ranging from 0.02 to 0.5 μmol P m^{-2} h^{-1} (Hines 1985; Charpy-Roubaud et al. 1996). Integrating these values for the duration period of the enclosure incubations, the potential P input through diffusional flux was then estimated as 0.1–0.5 μmol P m^{-2}, one order of magnitude lower than the pore-water reservoir of DRP. Holothurian selective sediment eaters, filter feeders, or both are responsible for bioturbation of sediments and supplying nutrients by excretion (Uthicke 1999), which probably increases the DRP flux. In our field observations, holothurians were found in the area of seagrass beds (Fig. 1) but were virtually absent in sand flat areas. No macrobenthic organisms were found during core sampling of sediments around station CL-550. Thus, the effect of macrobenthic organisms on the DRP flux from the sediment was probably not significant in the sand flat area.

The above calculations indicated that pore-water DRP and diffusional flux has a potential to supply P for the microphytobenthos production at the level of ~3 μmol P m^{-2} and 0.1–0.5 μmol P m^{-2}, respectively. The quantitative importance of these sources can be evaluated by comparing these P reservoirs with the P demands of microphytobenthic communities. There is little information on the stoichiometric relationship between P demand and C production in microphytobenthos metabolisms. The Redfield stoichiometry for C production and P utilization (106 : 1, Redfield 1958; Redfield et al. 1963) might be an index to estimate the P demands of microphytobenthic communities. Benthic diatoms, however, commonly produce large quantities of extrapolymeric carbohydrates (Smith and Underwood 1998) that are likely to elevate the C : P ratio. Furthermore, the microscopic observation and HPLC pigment analyses indicated the presence of Cyanophyta and Chlorophyta in the carbonate sediments that may have different C production or P utilization patterns from diatoms. Therefore, estimation based on the Redfield ratio may over- or underestimate the P demands of ambient microphytobenthic communities. The P demands estimated from C production using the Redfield ratio were then calculated as 19–48 μmol P m^{-2} h^{-1} in the enclosure experiments. This value is one or two orders of magnitude higher than P supplies from pore water and through diffusional flux estimated above. This suggests that both reservoirs, that is, pore-water DRP and diffusional flux, are not major sources of available P for the observed high production. Insignificance of these sources was directly shown by the results of the bottle incubation, in which the pore water in the used sediment sample had been previously washed with seawater just before the experiment (*see Materials and methods*); hence, no excess DRP was retained in the bottles. As well, other external sources of P, for example diffusional flux from the deeper layer, cannot be considered in the closed system of the bottle incubation. Thus, we could conclude that P associated with sediment particles, but not the dissolved fraction, could be the only possible source of available P that would supply enough for microphytobenthos production.

The extent and availability of P associated with sediment particles could be evaluated by the results of in situ bottle incubations and laboratory experiments. Considerable increases in DRP concentrations in the killed-control treatment of the bottle incubation (2.1 μM, Fig. 4) revealed that a large amount of DRP was released from sediment particles to the solution phase. The absence of DRP in the control bottle indicates that P release from sediment particles and P utilization by microphytobenthic communities mostly balanced each other. No difference in photosynthetic rates between the control and P-enriched bottles suggested that the DRP released from sediment particles was a useful source and its availability was comparable with that of the added DRP. Based on the chemical fractionation of P in marine sediments, the component easily released to the solution phase is known as P adsorbed (loosely sorbed or exchangeable P) on the sediment particles (Ruttenberg 1990; Jensen et al. 1998). For quantitative evaluation of the adsorbed P in the carbonate sediments, laboratory experimental data (Fig. 5B) were fitted to a Langmuir isotherm equation according to the protocol of Entsch et al. (1983).

$$P_{ads} = \frac{P_m b C}{1 + bC} \quad (1)$$

with

$$P_{ads} = P_m - P_{des} \quad (2)$$

P_{ads} is the amount of P adsorbed on sediment at each equilibrium, P_m is the limiting amount of adsorbed P at infinite C, b is a constant, C is the concentration of DRP in solution (μM) at each equilibrium, and P_{des} is the integral amount of P desorbed to solution. P_{ads}, P_m, and P_{des} are expressed as the concentration in sediments (μmol P g^{-1} dry wt). The equations can be rewritten as

$$P_{des} = \frac{P_m}{1 + bC} \quad (3)$$

The regression analysis for Eq. 3 using the values of P_{des} and C, which could be obtained directly from the experimental data, gave a fitted value of 0.39 ± 0.01 μmol P g^{-1} dry wt for P_m with a good correlation ($r^2 = 0.998$, $n = 14$, $P < 0.001$) as plotted in Fig. 6. This value corresponds to 5.5 and 6.6% of total and inorganic P, respectively, in the sediment sample examined. Entsch et al. (1983) reported lower abundance of P_m (<2% of total P) for coral reef sediment from Davis Reef in the Great Barrier Reef. The dif-

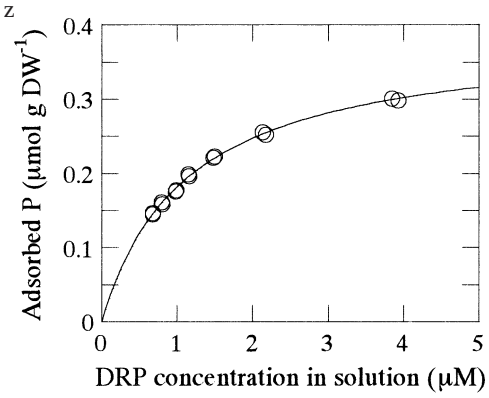

Fig. 6. The calculated Langmuir isotherm of P adsorbed on the sediment particles at different final concentrations of 24-h equilibrium. The regression line was drawn using Eq. 1 described in the text.

ference in the abundance of adsorbed P between our study and Entsch et al. (1983) is presumably due to differences in experimental design. Their estimate was based on a rapid equilibrium of 30 s, whereas we employed a 24-h equilibrium. As shown in Fig. 5A, the desorbed DRP concentration in seawater increased considerably as a function of time during the initial 10 h of the experiment. Thus, estimates of adsorbed P (P_m) should vary as a function of the length of equilibration period. Studies using a sequential extraction technique also showed that absorbed P is a minor component of P in some carbonate sediments—2% of total P in Bermuda (Jensen et al. 1998) and 5–7% of total P in French Polynesia (Harris et al. 2001). These results reveal that absorbed P is a quantitatively minor component of P reservoirs in the subtropical carbonate sediments.

Although adsorbed P is a relatively insignificant fraction of sedimentary P pools, the rapid exchange between sediment particles and solution (Fig. 5A) suggests this fraction is a useful source of P for microphytobenthos production. In the bottle incubation experiments, the enrichment of DRP did not enhance production (Fig. 4) because no considerable difference in DO production was found with or without the addition of DRP. This implies that photosynthetic production of microphytobenthic communities is not limited by the availability of adsorbed P. Assuming the photic zone in carbonate sediments develop to a depth of 4 mm, the total amount of the adsorbed P in this zone was 2.1 mmol P m^{-2}. This amount of P could sustain the organic C production of 220 mmol C m^{-2}, based on the Redfield ratio, which corresponds to a month of photosynthetic production of microphytobenthic communities estimated by the enclosure experiments. The standing stock of adsorbed P in the top 4 mm of the sediments corresponds to several months of the diffusional DRP flux (~12 μmol m^{-2} d^{-1}) estimated from the data of Charpy-Roubaud et al. (1996). Furthermore, the enormous amount of sediment below the photic zone is potentially significant, supplying available P through desorption and following diffusional flux to the photic zone on a longer timescale. Thus, the production of microphytobenthic communities can be maintained over long time scales with the extensive source of P accumulated in the carbonate sediment.

Cycling of phosphorus in the carbonate sediments—The results presented here show that a sedimentary pool of P, in particular adsorbed P, is one of the most important sources for microphytobenthic community production in carbonate sediments. Even though the carbonate sediments have a relatively large resource of this available P for maintaining productivity, there must be potential losses of P from the sediments through diffusional flux and desorption to the overlying seawater. However, laboratory and field researches showed that there is no net liberation of P from undisturbed coral reef sediments (Atkinson 1987). This suggests that there are other mechanisms to control P flux from sediments. Uptake of P by microphytobenthic communities at the SWI is one of the key mechanisms that retain the P resource in carbonate sediments. In the bottle incubation experiments, there was evidence of high efficiency of P uptake. The apparent amount of P uptake by microphytobenthic communities during the bottle incubation experiments could be estimated using changes in DRP concentrations (2.1–2.3 μM) in the P-enriched treatment and the killed-control experiments (Fig. 4). By comparing those results with photosynthetic carbon production in the control and P-enriched treatment (49.5 μM), the resulting C/P ratio is 22–24, indicating an excess utilization of P relative to the Redfield stoichiometry (C/P = 106). Some experimental and model studies have described ''luxury P uptake,'' where aquatic microorganisms are capable of incorporating and storing P above that required to meet metabolic demand (e.g., Portielje and Lijklema 1994; Baretta-Bekker et al. 1998). Under ambient conditions before sampling the bottle incubation experiments, some microphytobenthic communities in the sediments used had been exposed to overlying seawater, where the DRP concentration was extremely low. Such P-starved cells might actively incorporate excess amounts of DRP. This process is presumably one of the mechanisms of microphytobenthic communities, which is responsible for maintaining their high productivity and retaining P resources in coral reef sediments.

Although the diffusional flux of P from the sediments might be minimized by microphytobenthic metabolism, potential losses of P must be considered through some other physical and biological processes, including resuspension and grazing by sediment feeders. Unfortunately, there is no quantitative information regarding the removal P flux from the carbonate sediments of coral reefs through these processes. Considering the steady-state conditions observed, there must be some input fluxes of P to the sediments to compensate for the removal flux of P. Sedimentation of suspended particles and aged marine plants is an important source for supplying P to the sediments. The source materials of the carbonate sediments such as coral fragments and coralline algal skeletons are likely a significant P source in sediments as well. However, there is little quantitative information on the input flux of P to the carbonate sediments of coral reefs. As preliminary research for better understanding of the P cycle in coral reef ecosystems, we measured the chemical composition of P in the carbonate sediments and

these source materials. The results of chemical fractionation of P pools in these materials are compiled in Table 1. The results show that organic P is a minor P component accounting for 13.4 ± 1.7% ($n = 25$) of total P in the surface sediment samples. On the other hand, source organisms forming the carbonate sediments, namely, growing corals (*Acropora*, *Montipora*, *Heliopora*, *Pavona*, and *Porites*) and coralline algae (*Padina* sp., *Galaxaura* sp., and *Jania* sp.), contained a significant amount of organic P. Percentage of organic P/total P was 74.5% in the coral samples ($n = 42$) and 50.2% in the algae samples ($n = 17$). The considerable reduction in the abundance of organic P from these source organisms to the deposited sediments implies that a large fraction of organic P produced by the organisms had been readily remineralized before or at a very early stage of entering the sediments, or at both times. Invariability in organic P concentration throughout the sediment column (Fig. 2) suggested that remineralization of deposited organic P was insignificant within the observed depth layers. Reduced reactivity of organic P deposited in the sediments was also inferred by the constant value of the organic C/P ratio through the sediment column (Fig. 2), because the C/P ratio has been known to increase with organic matter decomposition (Ingall and Van Cappellen 1990; Clark et al. 1998). These results strongly indicate that the large fraction of organic P remaining in the carbonate sediments was composed of refractory materials that withstand early diagenetic mineralization. Therefore, from the point of availability as the P source for microphytobenthos production, organic P is the less important fraction; hence, inorganic P, in particular adsorbed P, should be the major source to sustain microphytobenthos production in the carbonate sediments of coral reefs.

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