

## Carbon flux by suspended and sinking particles around the barrier reef of Palau, western Pacific

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### *Abstract*

Suspended and sinking particles were studied around a barrier reef of the Palau Islands in the western Pacific. Concentrations of particulate organic carbon (POC), particulate organic nitrogen (PON), and chlorophyll *a* were high in reef waters and decreased toward the open ocean. At the reef edge, concentrations of organic particles in outgoing waters were higher than those in incoming waters, indicating net export of organic matter. Sediment trap observations conducted off the barrier reef showed a larger vertical flux of POC at an inshore station (2.5 km off the reef edge) than that at an offshore station (20 km), attributable to the net export of organic particles. Organic/inorganic carbon ratios of particles trapped at a depth of 45 m in the lagoon were smaller than those of suspended particles in surface water, suggesting a rapid decomposition of organic matter during sedimentation and a resuspension of carbonate-dominant bottom sediments.

We estimate that 7% of the gross community production in the reef is deposited in the lagoon zone, 4% is exported to the open ocean, and 0.6% is transferred below the thermocline (150 m depth) in the ocean.

The coral reef ecosystem is regarded as one of the most productive areas on earth and has received much attention since the pioneering work of Sargent and Austin (1949) and Odum and Odum (1955). To explain the extremely high productivity of coral reef ecosystems in a low nutrient environment, their organic materials are thought to be tightly recycled. Many studies, however, have estimated that such a coral reef has a net production of organic material (e.g.,

Smith 1973; Atkinson and Grigg 1984; Kayanne et al. 1995; Gattuso et al. 1996), some of which is presumably exported to the surrounding ocean (Hatcher 1983; Crossland et al. 1991). The export of organic particles from some reefs to the surrounding ocean has been reported (Marshall 1965; Johannes 1967; Quasim and Sankaranarayanan 1970; Charpy and Charpy-Roubaud 1991), but in general our knowledge of the influence of the reef on its adjacent sea is quite limited (Erez 1990). Kinsey (1985) stated that "Fluxes of particles entering and leaving coral reefs have been very inadequately studied though change in the concentrations of such materials are appreciable." Studies on carbon fluxes not only within coral reef areas but also between the reef and the surrounding ocean are necessary for understanding the carbon cycle in the entire coral reef ecosystem.

In this study, we measured suspended and sinking particles at a Palau Islands barrier reef in order to understand carbon flux between the reef and the open ocean. Horizontal and vertical distributions of suspended particles were examined at stations on a transect across the reef to the ocean, and their concentrations in incoming and outgoing waters at the reef edge were measured for evaluating the import and the export of such particulate matter through the reef. A sediment trap was also used to study the vertical flux of particulate materials inside and outside the reef.

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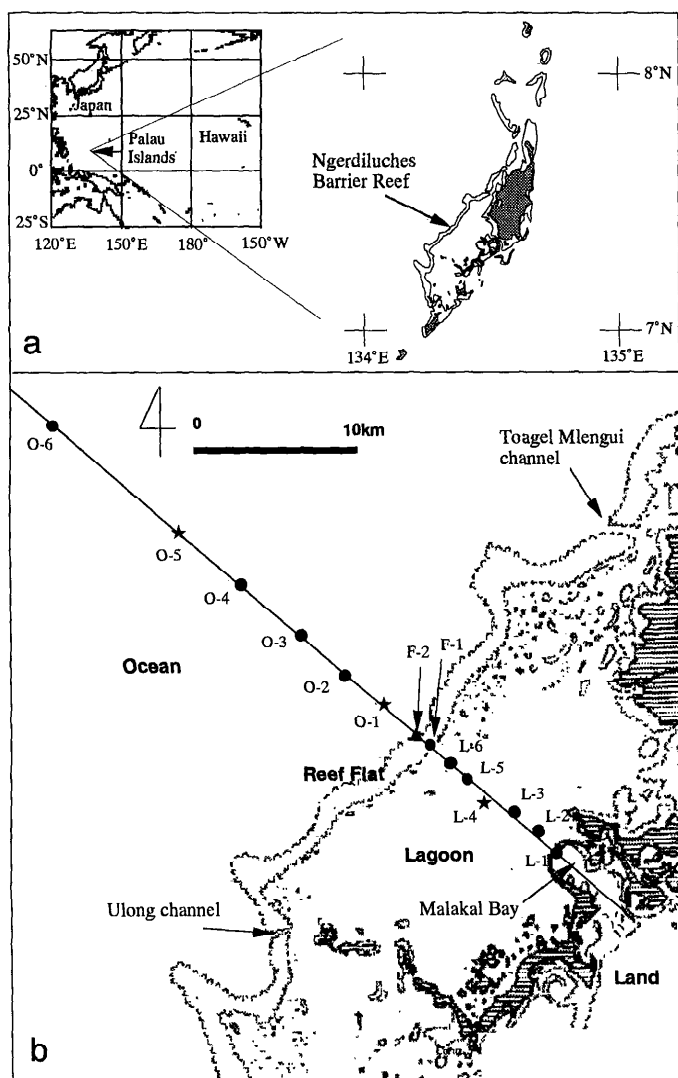


Fig. 1. (a) Location of Palau Archipelago in the western Caroline Islands; (b) sampling stations made in the Ngerdiluches barrier reef; (●) stations for surface water sampling; (▲) reef edge station for flood and ebb water sampling; and (★) stations for vertical water sampling, CTD measurements, and sediment trap deployments.

## Materials and methods

**Study area**—Field observation was carried out in July 1994, and in July–August 1995, at a barrier reef of the Palau (Belau) Archipelago, Caroline Islands, West Pacific, during expeditions of RV *Sohgen-maru*. This archipelago forms a gentle arc ( $6^{\circ}53'N$  to  $8^{\circ}12'N$  and  $134^{\circ}08'E$  to  $134^{\circ}44'E$ ) (Fig. 1a), and our investigations were performed at the Ngerdiluches barrier reef, located at its western side (Fig. 1b), where the barrier reef platform extends over 80 km in length. The detailed topography of the Palau reef was described by Maragos and Cook (1995).

The Ngerdiluches barrier reef area can be divided into three major zones: lagoon, barrier reef flat, and ocean. It has only one deep channel, Toagel Mlungui, with a maximum depth of 65 m. The entire southwestern side of the barrier

reef platform lacks passes except for the dredged German Channel near the southwestern end (Maragos and Cook 1995) and a small gap, Ulong Channel, between Toagel Mlungui and German Channel (Fig. 1b). Six research stations were made on a transect across the lagoon zone, plus two in the reef flat zone and six in the open ocean (Fig. 1b). The transect was set parallel to the current direction observed on the reef flat. The width of the lagoon zone on the transect was about 12 km. The mean depth of the lagoon was 20 m, and the maximum depth in this area is 55 m. The barrier reef flat zone was about 1.5 km in width. The nearest research station in the ocean zone was 2.5 km from the reef edge, and the furthest site was 30 km away.

**Environmental factors**—Current speed, salinity, water temperature, and tides were monitored continuously at the stations on the reef flat during 15–22 July 1994. Details of methods and results have been described by Suzuki (1995). The current was unidirectional, to-and-fro, during flood and ebb tides. The most swift current, reaching  $50 \text{ cm s}^{-1}$ , was observed at Sta. F-2 (Suzuki 1995). Volume transport was calculated from current velocity and water depth. Vertical profiles of salinity and temperature were measured at Sta. L-4 in the lagoon and Sta. O-1 and O-5 in the ocean by using a conductivity-temperature-depth (CTD) profiler (model AST-500, Alac Electronics). CTD measurements at Sta. L-4 were conducted every day from 12 to 29 July 1995, whereas those at Sta. O-1 and O-5 were made on 1 and 2 August 1995.

**Sampling procedures**—Surface water samples at the reef stations were collected in the daytime during ebb tide on 27 July 1995 and at the ocean stations on 1 and 2 August 1995. Vertical water samples were also taken at Sta. L-4 in the lagoon and Sta. O-1 and O-5 in the ocean. Additional surface water samplings at Sta. L-4 were carried out at other times in 1994 and 1995, and samples of flood and ebb waters were also collected at the reef edge (Sta. F-2). For analyses of particulate materials, 10 liters of surface water was collected in a polyethylene container; another 1 liter was collected for the determination of chlorophyll *a* (Chl *a*). Filtration was carried out in the ship's laboratory. For measurements of particulate organic carbon (POC) and particulate organic nitrogen (PON), the samples were filtered through a 24-mm-diameter glass-fiber filter (GF/F, Whatman) that had been previously heated in air at  $450^{\circ}\text{C}$  for 4 h to destroy organic material. Ten liters of samples were filtered for the analyses of POC and PON. The filters were rinsed with filtered seawater (passed through a  $0.2\text{-}\mu\text{m}$  Millipore filter) and stored at  $-20^{\circ}\text{C}$ . For the analysis of Chl *a*, 1 liter of the sample was filtered through a GF/F, which was then wrapped in aluminum foil and stored at  $-20^{\circ}\text{C}$ .

**Sinking particles and bottom sediments**—Cylindrical sediment traps were set at Sta. L-4 in the lagoon from 12 to 16 July 1994 and from 12 to 24 July 1995, and at Sta. O-1 and O-5 in the ocean on 1 and 2 August 1995. At the lagoon site (Sta. L-4), paired traps were placed at 45-m depth (about 10 m above the bottom) in 1994 and at 20- and 45-m depth in 1995. The ratio of height of trap to width of opening was

3:1 (48 × 16 cm, about 9.6 liters in volume), as recommended by Gardner (1980), and particles were collected in a 300-ml polyethylene bottle attached to the bottom of the trap. Prior to deployment, each trap was filled with filtered seawater (through a 0.45- $\mu\text{m}$  Millipore filter) to which 25 g liter<sup>-1</sup> NaCl was added to increase the density, as recommended by Knauer et al. (1979). One of each pair of trap bottles contained 1% neutralized formaldehyde in seawater. The traps were fastened to an anchored Kevlar rope connected to a subsurface float submerged at 5-m depth. A small surface float was attached to the subsurface buoy for retrieval. Trapped particles were collected every 48 h. The poisoned sample bottles were sealed, stored at 4°C, and brought back to the laboratory in Japan for the analyses of carbon and nitrogen. The unpoisoned samples were filtered onto 47-mm-diameter GF/F and stored at -20°C for measurement of Chl *a*.

At the ocean sites (Sta. O-1 and O-5), the paired traps were set at 50- and 150-m depth, and 10 traps fixed on a stainless steel frame were set at 300-m depth. The traps were kept vertical by a Kevlar rope with a sinker and surface floats. The setting was maintained by a small boat with a global positioning system (GPS, model IPS-30, Sony). The traps were left for about 6 h during ebb tide in daytime. Recovered sample bottles were treated in the same way. All the bottles were poisoned with neutralized formaldehyde solution (final concentration 1%) for analyses of carbon and nitrogen.

Samples of the bottom sediments collected at the lagoon site (Sta. L-4) were also stored at -20°C, and the contents of POC, particulate inorganic carbon (PIC), and PON were later analyzed in the laboratory.

**Analytical procedures**—Filtered samples of suspended particles were dried in a vacuum desiccator prior to the analysis. Trapped samples in the bottles were filtered through 1-mm stainless steel mesh to remove visiting organisms and large particles. Trapped particles were then filtered through preweighed GF/F (preheated at 450°C for 4 h). Some visible zooplankton that passed through the 1-mm mesh were also removed from the filter using tweezers. Three randomly selected trap bottles collected at 300-m depth were pooled because the amount of trapped material was so small. The materials on the filters were rinsed with 50 ml of distilled water to remove remaining salts, dried at 50°C for over 48 h, and then weighed.

Organic carbon and nitrogen contents of suspended and trapped particles on the filters were analyzed with a carbon-hydrogen-nitrogen (CHN) analyzer (model MT-5, Yanaco). Combustion was at 795°C for 5 min, and the bridge current for the detector was set at 100 mA for carbon and 180 mA for nitrogen.

To remove inorganic carbon (carbonate), the samples were exposed to HCl vapor at room temperature (Yamamuro and Kayanne 1995) for 24 h in a 3-liter glass desiccator containing 100 ml of 12 N HCl. It was noted that this acid treatment often increased the organic carbon in blanks with no effect on nitrogen contents (Sharp, 1974). The increased value due to HCl treatment for 24 h on 24-mm GF/F was about 0.5–1.0  $\mu\text{mol C}$ , although the cause of this increase

is not yet clear. Considering the average concentration of POC (roughly 3  $\mu\text{mol liter}^{-1}$ ), filtration of a 10-liter sample resulted in about 30  $\mu\text{mol POC}$  on the filter. Although this value, increased by acid treatment, was <4% of the POC on the filter, we corrected the C values by subtracting the value of a blank filter treated in the same way in each analysis.

Filter samples not treated with HCl vapor were used for estimates of total carbon, and PIC content was calculated from the difference between values of total and organic carbons.

The combustion efficiency of carbonates using the CHN analyzer was studied under the analytical conditions. The carbon released from CaCO<sub>3</sub> (Wako Chemicals) was measured against an antipyrine standard (Kishida Chemical). Over 99% of the carbon in CaCO<sub>3</sub> was released as CO<sub>2</sub> under the analytical conditions used.

Chl *a* was extracted by soaking the frozen filters in 10 ml of N,N-dimethylformamide at -20°C for 24 h in the dark. The Chl *a* content was measured with a spectrofluorometer (model FP-77, Japan Spectroscopic) against standard Chl *a* solutions (Sigma Chemical). When the concentration was too high for the spectrofluorometer, it was measured using a spectrophotometer (model UV-160A, Shimadzu), using the formula given by Moran (1982).

## Results

**Horizontal distributions of suspended particles**—Concentrations of POC, PON, and Chl *a* in reef waters were 3.33–5.63  $\mu\text{mol C liter}^{-1}$ , 0.50–1.00  $\mu\text{mol N liter}^{-1}$ , and 0.36–0.62  $\mu\text{g liter}^{-1}$ , whereas those in ocean waters were 3.20–4.56  $\mu\text{mol C liter}^{-1}$ , 0.37–0.54  $\mu\text{mol N liter}^{-1}$ , and 0.10–0.23  $\mu\text{g liter}^{-1}$ , respectively. Concentrations of these particles decreased from the reef toward the ocean (Fig. 2a,c,d). On the other hand, concentrations of PIC were high around the reef flat. The maximum was recorded at Sta. F-2 (3.41  $\mu\text{mol liter}^{-1}$ ), and the concentrations decreased from the reef flat toward both the lagoon and the ocean (Fig. 2b). The C/N ratios of the suspended particles in the lagoon waters ranged from 6.3 to 7.4, whereas those in ocean waters ranged from 7.1 to 9.0 (Fig. 2e). The Chl *a*/POC ratios were greater in the lagoon waters ( $6.8\text{--}9.9 \times 10^{-3}$ ) than those in ocean waters ( $2.6\text{--}5.1 \times 10^{-3}$ ) (Fig. 2f).

**Vertical distributions of suspended particles**—CTD profiles in the ocean showed that the surface mixed layer was about 50 m in thickness (Fig. 3). A thermocline was observed below the surface mixed layer between 50- and 150-m depth. No distinct thermocline was observed in the lagoon, where the depth was 55 m (Sta. L-4). In the vertical distributions of POC and PON at Sta. L-4, the maximum values were observed at 10-m depth (Fig. 4a,c). On the other hand, their maxima were observed at 50 m depth at the ocean stations (Sta. O-1 and O-5). The concentrations of POC and PON at the inshore station (Sta. O-1) were higher than those at the offshore station (Sta. O-5). The concentrations of PIC at the lagoon station increased with depth from 10 to 50 m, whereas no such trend was observed at the ocean stations (Sta. O-1 and O-5) (Fig. 4b). Chl *a* maxima were observed at the depths of 40 m at Sta. L-4, 50 m at Sta. O-

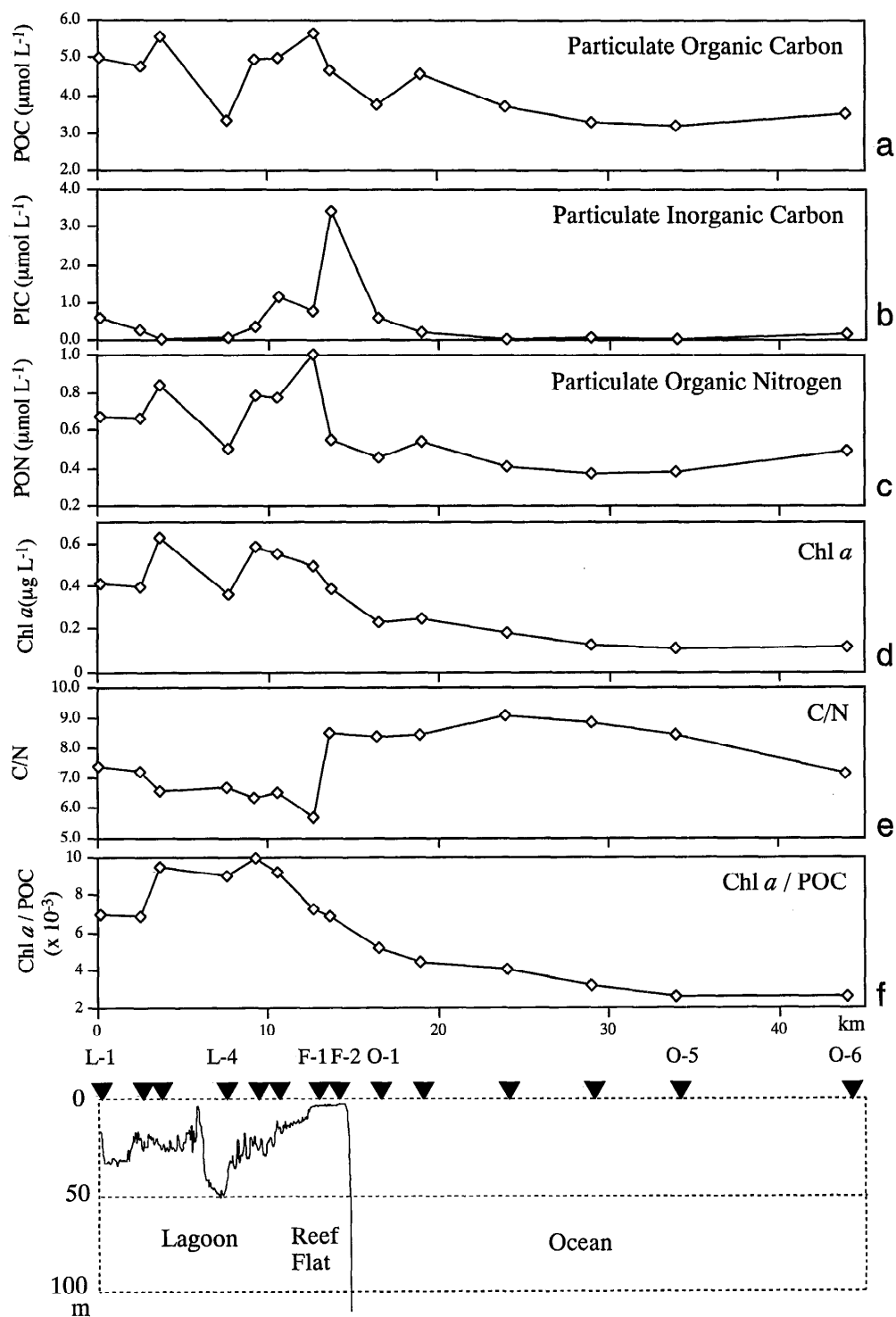


Fig. 2. Horizontal distributions of particulate organic carbon (POC), particulate inorganic carbon (PIC), particulate organic nitrogen (PON), chlorophyll *a* (Chl *a*), POC/PON ratio, and Chl *a*/POC ratio around the Palau barrier reef. Measurements at lagoon and reef flat stations were conducted on 27 July and at ocean stations on 1 and 2 August 1995, respectively.

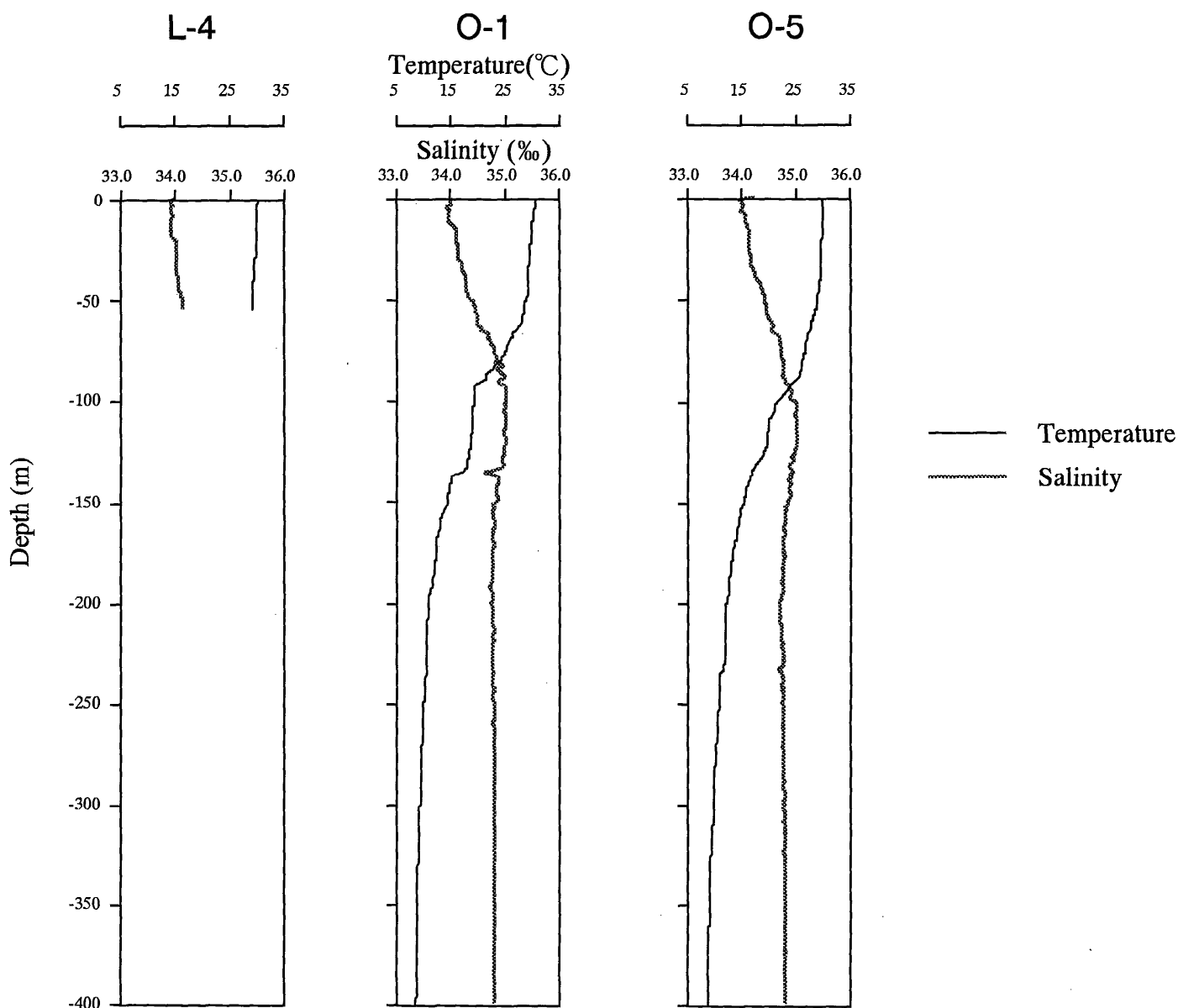


Fig. 3. Profiles of temperature and salinity at the study sites. Measurements at Sta. L-4, O-1, and O-5 were conducted 27 July, 1 and 2 August 1995, respectively.

1, and 100 m at Sta. O-5, where the respective concentrations were  $0.62$ ,  $0.44$ , and  $0.59 \mu\text{g liter}^{-1}$  (Fig. 4d). The C/N ratios at Sta. L-4 ranged from 5.7 to 7.0. These values were lower than those at the ocean stations: 7.7–11.2 at Sta. O-1 and 6.5–12.1 at Sta. O-5 (Fig. 4e).

The maximum Chl *a*/POC ratio ( $23.1 \times 10^{-3}$ ) was observed at 100-m depth at Sta. O-5, whereas the ratio at 50-m depth at the lagoon station was higher than those at the ocean stations (Fig. 2f).

*Import and export of the suspended particles at the reef edge*—The average ( $\pm$ SD) concentrations of organic particles in outgoing (ebb) waters,  $4.95 \pm 1.17 \mu\text{mol POC liter}^{-1}$ ,  $0.69 \pm 0.21 \mu\text{mol PON liter}^{-1}$ , and  $0.33 \pm 0.16 \mu\text{g Chl } a \text{ liter}^{-1}$  ( $n = 13$ ) significantly exceeded ( $p < 0.01$ ) those in

incoming (flood) waters:  $3.06 \pm 0.74 \mu\text{mol POC liter}^{-1}$ ,  $0.41 \pm 0.10 \mu\text{mol PON liter}^{-1}$ , and  $0.14 \pm 0.06 \mu\text{g Chl } a \text{ liter}^{-1}$ , respectively ( $n = 13$ ).

*Sinking particles in the lagoon*—Vertical fluxes of POC, PIC, PON, and Chl *a* at lagoon station are shown in Table 1. Fluxes at 45-m depth showed higher values and more day-to-day variation than those at 20-m depth (Fig. 5). The sedimentation rates of PIC rose markedly from 6.7 to 208.2  $\text{mmol m}^{-2} \text{d}^{-1}$  after 16 July 1995. After wind speeds reached  $5 \text{ m s}^{-1}$  during July 14–16 1995, the profiles of sigma-t ( $\sigma_t = (\rho - 1) \times 1000$ , where  $\rho$  is the density of seawater) changed drastically (Fig. 5b,c). The mooring system for the traps was destroyed during 14–16 July 1995. Although the

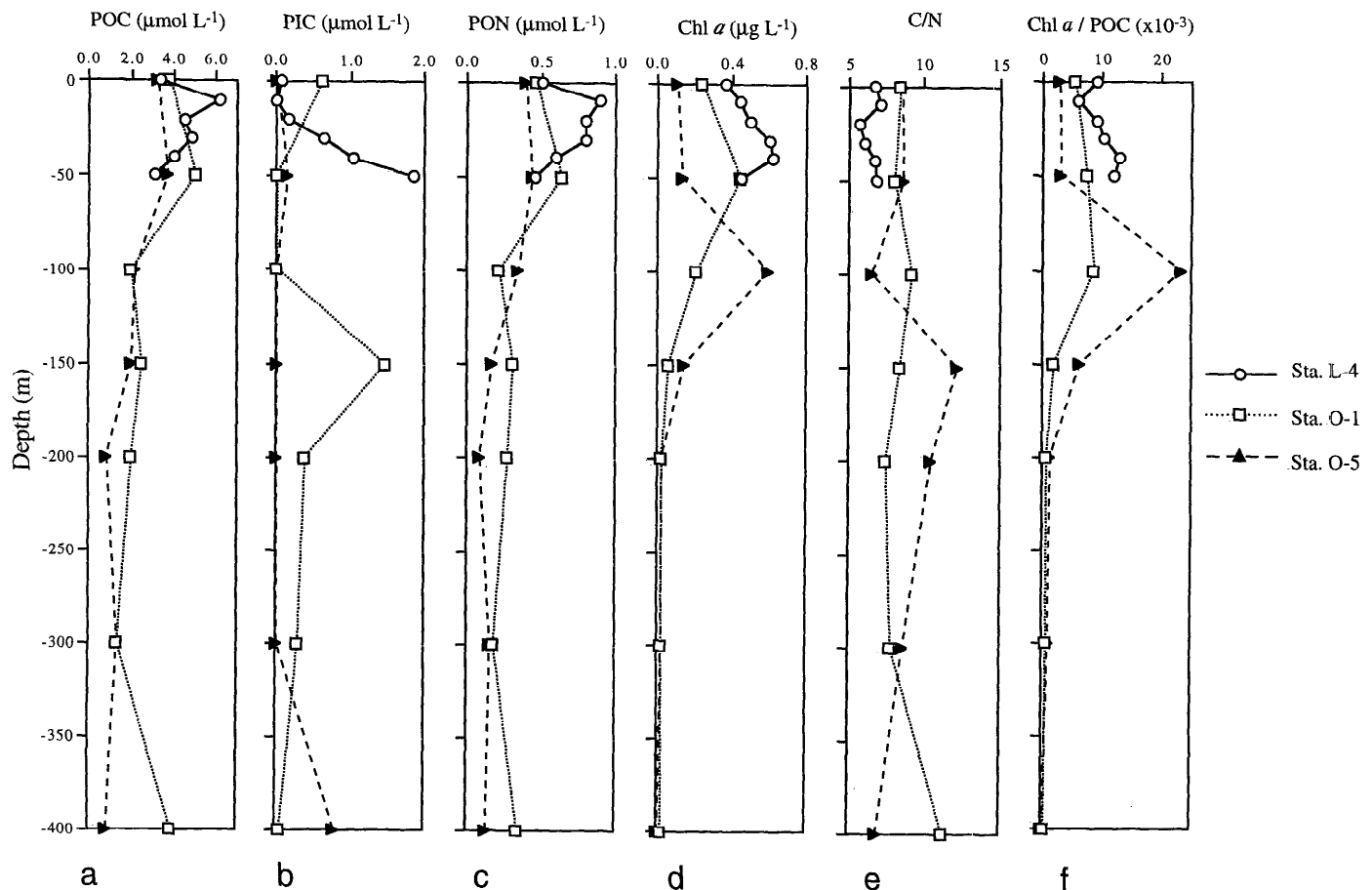


Fig. 4. Vertical distributions of POC, PIC, PON, Chl *a*, POC/PON ratio, and Chl *a*/POC ratio at the study sites. Measurements at Sta. L-4, O-1, and O-5 were conducted on 27 July, 1 and 2 August 1995, respectively.

Table 1. Vertical fluxes of particulate organic carbon (POC), inorganic carbon (PIC), organic nitrogen (PON), and chlorophyll *a* (Chl *a*) observed at the lagoon and the ocean stations. The given values are the mean and the SD (in parentheses).

Station	Depth, in m (number of samples)	POC	PIC	PON	Chl <i>a</i>
		(mmol m <sup>-2</sup> d <sup>-1</sup> )			(mg m <sup>-2</sup> d <sup>-1</sup> )
L-4 (lagoon)	-20	6.11	3.09	1.03	0.33
	( <i>n</i> = 4)	(1.02)	(1.23)	(0.06)	(0.22)
	-45	20.92	96.84	1.87	1.19
	( <i>n</i> = 7)	(11.97)	(74.41)	(0.83)	(0.32)
O-1 (inshore; 2.5 km from the reef front)	-50	1.08	0.14	0.15	ND*
	( <i>n</i> = 2)	(0.39)	(0.15)	(0.04)	
	-150	0.53	0.57	0.07	ND
	( <i>n</i> = 2)	(0.16)	(0.01)	(0.02)	
O-5 (offshore; 20 km from the reef front)	-300	0.40	0.18	0.03	ND
	( <i>n</i> = 3)	(0.03)	(0.06)	(0.00)	
	-50	0.55	0.34	0.10	ND
	( <i>n</i> = 2)	(0.02)	(0.23)	(0.01)	
O-5 (offshore; 20 km from the reef front)	-150	0.35	0.30	0.06	ND
	( <i>n</i> = 2)	(0.05)	(0.23)	(0.00)	
	-300	0.19	0.10	0.03	ND
	( <i>n</i> = 3)	(0.06)	(0.03)	(0.01)	

\* ND, not determined.

mooring system was repaired after that accident, the fluxes became larger, especially at 45-m depth (Fig. 5e).

Chemical characteristics of suspended, trapped, and sedimented particles are summarized in Table 2. The contents of POC, PON, and Chl *a* were highest in the trapped particles at 20-m depth and lowest in the bottom sediments, whereas the C/N ratios were highest in the bottom sediments and lowest in the trapped particles at 20-m depth. The content of PIC (mg g<sup>-1</sup> dry weight) in the particles increased with depth from 9.8 (suspended particles in surface water) to 103.1 (bottom sediments), and the POC/PIC ratio decreased from 4.6 to 0.07.

*Sinking particles in the ocean*—As shown in Table 1, vertical fluxes of POC and PON at both of the ocean stations (Sta. O-1 and O-5) decreased with depth. The fluxes were larger at all depths of the inshore station (Sta. O-1, 2.5 km from the edge) than those of the offshore station (Sta. O-5, 20 km from the edge). The flux of PIC also decreased with depth at Sta. O-5, whereas the maximum flux was observed at 100-m depth at Sta. O-1.

## Discussion

*Export of particulate organic materials from the reef to the open ocean*—POC, PON, and Chl *a* from the surface to

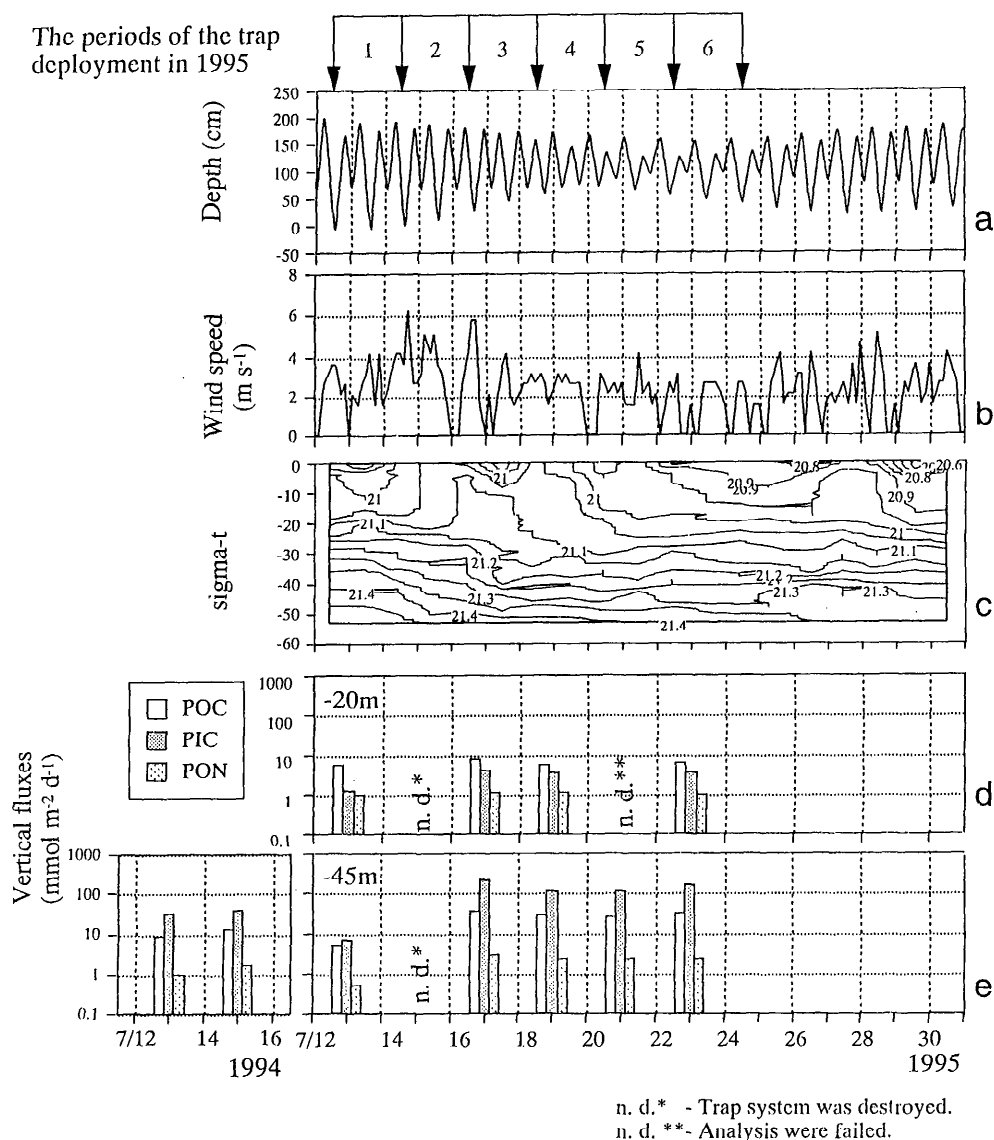


Fig. 5. Time series of water depth, wind speed at Koror, sigma-t monitored at the Sta. L-4, and the vertical fluxes of POC, PIC, and PON at 20- and 45-m depths at Sta. L-4. The data on water depth and wind speed originated from a tide table and a report of local climatological data by the National Oceanic and Atmospheric Administration (NOAA).

Table 2. Chemical characteristics of suspended, trapped matters and bottom sediments at Sta. L-4 in the lagoon. The given values are the mean and the SD (in parentheses).

	POC*	PIC	PON	Chl <i>a</i>	POC/PIC	C/N	Chl <i>a</i> /POC
	(mg g <sup>-1</sup> DW)			(mg g <sup>-1</sup> DW)	(molar ratio)		( $\times 10^{-3}$ )
Suspended matter (0 m; <i>n</i> = 10)	66.9 (16.0)	9.8 (5.4)	10.4 (2.6)	0.39 (0.11)	4.6 (1.6)	7.7 (1.3)	6.7 (2.2)
Trapped matter (20 m; <i>n</i> = 4)	128.7 (21.5)	65.1 (25.9)	25.3 (1.5)	0.51 (0.36)	2.4 (1.3)	6.0 (0.9)	4.3 (2.4)
Trapped matter (45 m; <i>n</i> = 7)	21.1 (12.1)	97.7 (75.1)	2.2 (1.0)	0.09 (0.03)	0.3 (0.2)	10.6 (2.0)	5.4 (3.0)
Bottom sediments (55 m; <i>n</i> = 2)	7.0 (0.4)	103.1 (0.1)	0.03 (0.00)	ND	0.07 (0.02)	17.0 (1.0)	ND

\* POC, particulate organic carbon; PIC, particulate inorganic carbon; PON, particulate organic nitrogen; Chl *a*, chlorophyll *a*; DW, dry weight; ND, not determined.

Table 3. Sedimentation rates in various reefs.

Study site	Depth, in m (bottom)	POC*	PON	CN ratio (molar ratio)	POC in reef water	Reference
		(mg m <sup>-2</sup> d <sup>-1</sup> )			(mg m <sup>-3</sup> )	
Palau, Caroline Islands	20 (55)	73.4	14.4	6.0	55.9	This study
	45 (55)	251.2	26.2	10.6		
Kaneohe Bay, Hawaii One Tree Island, GBR	10 (14.5)	450	59	9.4	209.0†	Taguchi (1982)
	1.2 (1.2)	3,900	38	40		
	3.0 (3.0)	1,500	40	32		
	4.5 (4.5)	1,400	39	29		
Tikehau Atoll, French Polynesia	15 (19)	350		11.2	136.9	Charpy and Charpy-Roubaud (1991)
Davies Reef, GBR	2–13 (5–27)	9.2–141	36	7.6		Hansen et al. (1992)
New Caledonia	9–26 (11–28)	481–1,157	20–38	19–30	190–268	Clavier et al. (1995)

\* POC, particulate organic carbon; PON, particulate organic nitrogen; GBR, Great Barrier Reef.

† Data from Smith et al. (1981) observed at the same site (south sector of Kaneohe Bay) and the same periods (1978).

50-m depth decreased from the reef toward the ocean (Figs. 2, 4). Similar trends were also reported at Eniwetok Atoll (Marshall 1965; Johannes 1967), Kavaratti Atoll (Quasim and Sankaranarayanan, 1970), and Tikehau Atoll (Charpy and Charpy-Roubaud, 1991). At the edge of the reef, the concentrations of POC, PON, and Chl *a* showed significant differences between incoming and outgoing waters. These results present quantitative data for the export of organic particles from the reef to the surrounding ocean. The vertical fluxes of POC and PON at the inshore station (Sta. O-1) were higher than those at the offshore station (Sta. O-5) (Table 1), indicating that some of the particles exported from the reef were trapped as sinking particles at the inshore station.

*Origin of particulate materials*—Microscopic observations of the suspended materials showed that most of the suspended matter was composed of amorphous materials. Phytoplankton and algal fragments were also found.

The C/N ratios of organic particles may give some insight into their origins. The C/N ratios of the suspended particles in lagoon waters of the Palau reef ranged from 6.3 to 7.4. The C/N ratios of phytoplankton range between 6 and 8 (Parsons et al. 1961), whereas those of benthic marine plants are around 20 (Atkinson and Smith 1983). Johannes (1967) suggested the contribution of mucus released by corals to suspended particles, of which C/N ratios range from 6.9 to 13.7 for fluid mucus and from 4.8 to 5.9 for mucous sheets (Coffroth 1990). On the other hand, the C/N ratio of terrestrial vascular plants is over 30 (Alexander 1977).

According to the C/N ratios of the suspended particles in lagoon waters of the Palau reef (6.3–7.4), the suspended particles are thought to be derived from reef organisms. The effect of vascular plants is thought to have been small in Palau reef during the study period.

The average C/N ratios of trapped particles in Palau reef were 6.0 and 10.6 at 20- and 45-m depth, respectively (Table 2). Relatively large variation in C/N ratios has been reported for trapped particles in coral reef regions (Table 3). The highest values (29–40), found at One Tree Island, in the Great Barrier Reef (Koop and Larkum 1987), might be partially related to overestimation of organic carbon; the authors

did not remove carbonates before their analysis, and they estimated organic carbon as 50% of the ash-free dry weight.

Variations in the C/N ratios of trapped particles might be attributed to the origin of the organic particles. Clavier et al. (1995) also reported higher C/N ratios for trapped particles (19–30) in New Caledonia and suggested that the contribution of terrestrial plants was larger than that of plankton-derived organic matter. On the other hand, in south sector of Kaneohe Bay, Hawaii, where phytoplankton dominates (Smith pers. comm.), low C/N ratios of trapped particles (9.4) were reported (Taguchi 1982). Hansen et al. (1992) also found low C/N ratios (7.6) of trapped particles in Davies Reef, in the Great Barrier Reef, and the main source of trapped particles was inferred to be benthic algae (C/N ratio = 14) on the reef flat. In Tikehau Atoll (Tuamotu Archipelago, French Polynesia), the C/N ratio of the trapped particles was 11.2. Charpy and Charpy-Roubaud (1991) reported that most of the detritus pool (84% of the POC) in Tikehau Atoll originated from lagoonal primary production, with the rest coming from the reef flat.

It seems that the C/N ratio in trapped particles is high when the material has terrestrial origins, whereas it is low when the material has reef origins. The data for Palau reef obtained in this study (6.0–10.6) are low, suggesting that the trapped particles originated from reef, not terrestrial, organisms.

As for the carbonate particles in reef waters, resuspension of bottom sediments is thought to be the main source. The concentration of PIC increased with depth at the lagoon site (Fig. 4b), suggesting the resuspension of carbonate-dominant bottom sediments. The maximum concentration of PIC in surface water was recorded at the reef flat site (Fig. 2b), where the resuspension seemed to be caused by the swift current.

*Sedimentation rate in the lagoon*—In the lagoon site, larger fluxes and variations in sedimentation rate at greater depths (45 m) can be attributed to the resuspension of material from the bottom sediments. Resuspended materials may increase the fluxes manifold, and they cause a major problem in shallow waters, where currents are strong. Vertical mixing is largely attributable to strong turbulence

Table 4. Estimation of diurnal community production rates and POC budget in the Palau barrier reef.

		Gross production rate (Pg)		Net production rate (Pn)	Lateral flux of POC*		Vertical flux of POC, in m			
		Planktonic	Benthic		Import	Export	20	50	150	300
Lagoon	mmol m <sup>-2</sup> d <sup>-1</sup>	25†	NM	NM			6.1			
	mol m <sup>-1</sup> d <sup>-1</sup> ‡	300					73			
Reef flat	mmol m <sup>-2</sup> d <sup>-1</sup>		760§	167§						
	mol m <sup>-1</sup> d <sup>-1</sup>		760	167	37	74				
Inshore	mmol m <sup>-2</sup> d <sup>-1</sup>	NM		NM				1.1	0.5	0.4
	mol m <sup>-1</sup> d <sup>-1</sup> ¶							13	6	5
Offshore	mmol m <sup>-2</sup> d <sup>-1</sup>	NM		NM				0.6	0.4	0.2
	mol m <sup>-1</sup> d <sup>-1</sup> ¶							7	4	2

\* POC, particulate organic carbon; NM, not measured.

† Averaged production rate for coral reef lagoons (Kinsey 1985).

‡ Lineal rate calculated from lagoon width of 12 km.

§ Data from Ikeda et al. (1997).

|| Lineal rate calculated from productive area of reef flat width of 1 km.

¶ Lineal rate considered from 12 km zones.

caused by processes such as tidal forcing, wind stress, variations in surface buoyancy flux, and other circulation processes (Demers and Therriault 1987). Disturbance of the lagoon water on 16 July (Fig. 5c) might have been caused by the strong winds (>5 m s<sup>-1</sup>) observed between 14 and 16 July 1995 (Fig. 5b), when the fluxes of trapped particles at 45-m depth were drastically increased. Sediment trap experiments are well known to vary from time to time (e.g., Deuser and Ross 1980; Honjo 1982). Although a series of long-term sediment trap studies is needed to characterize the year-round fluxes, we can estimate the vertical fluxes during the study period (July–August 1995).

*Fate of particulate materials in the lagoon*—The sedimentation rates of POC reported here were lower than those

from other studies of coral reef lagoons (Table 3), probably because of the lower concentrations of POC in the reef waters of Palau. Clavier et al. (1995) reported that in New Caledonia the sedimentation pattern was related to the concentrations of suspended particles. The depth of trap deployment may be another factor. In this study, traps were set at 20 and 45 m, considerably deeper than in other studies. Degradation of organic matter in the water column during sedimentation might be one of the important factors affecting the vertical flux of organic carbon in the lagoon.

POC/PIC ratios in the trapped particles from the lagoon were smaller than those of suspended particles in the surface water (Table 2), suggesting rapid decomposition of organic matter during sedimentation and resuspension of carbonate-dominant bottom sediments.

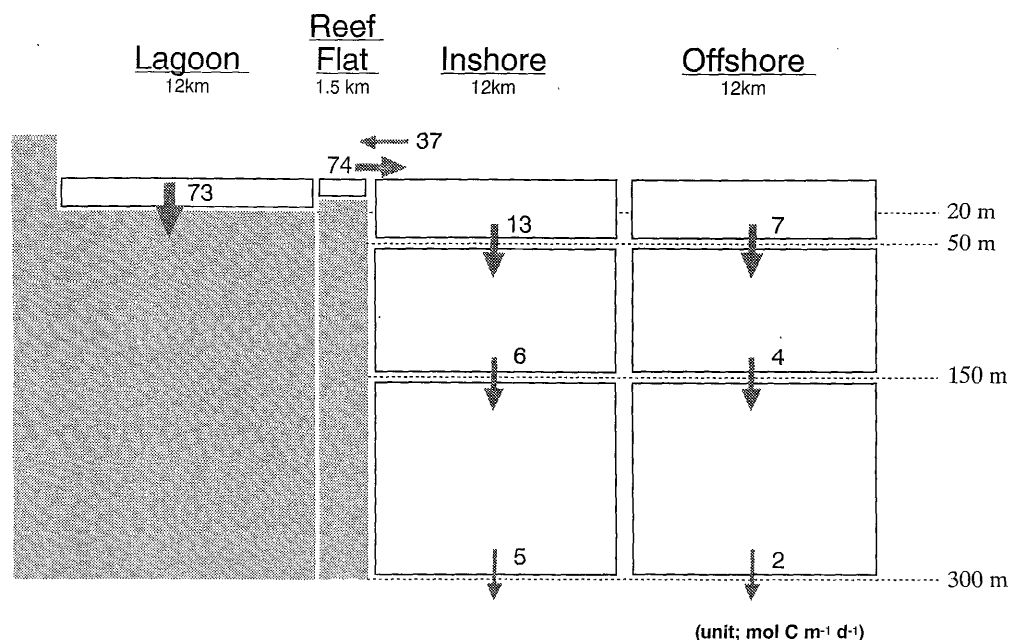


Fig. 6. Schematic diagram of POC flux in the Palau reef (see Table 4).

*POC budget around the Palau barrier reef*—The daily POC budget for the Palau reef was examined (Table 4, Fig. 6). The calculation included only fine particles (<1 mm). An evaluation of the fluxes that includes the fraction of larger particles may be important (Altabet et al. 1992), but this remains to be studied in Palau reef.

The entire coral reef area is composed of the reef (lagoon and reef flat) and the ocean (inshore and offshore). The average width of the lagoon in the study area is 12 km, so we compared it with zones of 12-km width inshore and offshore. The width of the productive area of the reef flat where living coral and seagrass predominate was taken to be 1 km.

Ikeda et al. (1997) reported that the gross community production rate of the reef flat in Palau was  $760 \text{ mmol m}^{-2} \text{ d}^{-1}$ . The production rate of phytoplankton in the lagoon of Palau reef was reported by Motoda (1969) as  $7.5 \text{ mmol m}^{-2} \text{ d}^{-1}$ ; this estimate used the data for Chl *a* and light penetration given by the formula cited by Ryther and Yentsch (1957). The average concentration of Chl *a* in lagoon water at 0–20-m depth in the Motoda (1969) study was  $0.19 \mu\text{g liter}^{-1}$ , which is almost half that of the present study (average  $0.43 \mu\text{g liter}^{-1}$ ). One reason for this discrepancy is thought to be the 30- $\mu\text{m}$  mesh size used in the filtration (Motoda 1969); a 0.7- $\mu\text{m}$  mesh was used in the present study. Considering the Chl *a* data, it is reasonable that the production rates of phytoplankton in Palau reef would be at least twofold those of the report by Motoda (1969). According to Kinsey (1985), the average gross production rate of phytoplankton in reef water is  $0.3 \text{ g C m}^{-2} \text{ d}^{-1}$  ( $25 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ). This value is adopted as the production rate in the lagoon. The estimation of net community production rate is thought to be important because there must be sufficient carbon fixation to provide for community respiration within the system before any carbon can be exported. Ikeda et al. (1997) reported the net community production rate of the reef flat in Palau as  $167 \text{ mmol m}^{-2} \text{ d}^{-1}$ , but data from the lagoon are not available at present (Table 4). In the present study, the carbon budget was calculated by using the gross community production rate. An estimation of the community production rate in the lagoon at Palau reef will be needed in the future.

From the data reported by Ikeda et al. (1997) and Kinsey (1985), the gross community production rate (Pg) in the reef was estimated to be  $1,060 \text{ mol C m}^{-1} \text{ d}^{-1}$ , which was sum of the production rates at the reef flat and lagoon zones.

The POC flux at the reef edge was calculated by multiplying the average POC concentration in flood ( $3.06 \mu\text{mol C liter}^{-1}$ ) and ebb water ( $4.95 \mu\text{mol C liter}^{-1}$ ) by the mean water volume transport at the site (Suzuki 1995). The import and export of POC were calculated to be 37 and  $74 \text{ mol C m}^{-1} \text{ d}^{-1}$ , respectively (Table 4), resulting in a net export of  $37 \text{ mol C m}^{-1} \text{ d}^{-1}$ , equivalent to about 4% of the Pg of the coral reef area. This value is comparable with that of other reefs. Taguchi (1982) reported that 6% of Pg was exported out of Kaneohe Bay, Hawaii; this was calculated from data on production, respiration, and sedimentation rates. Charpy and Charpy-Roubaud (1991) calculated the average POC export at Tikehau Atoll to be 6% of phytoplankton production. ECOPATH, one of the most comprehensive material flux models, also suggested that at French Frigate Shoals, Ha-

waii, up to 6% of Pg may be permanently lost via sediment burial or export to the ocean (Atkinson and Grigg, 1984).

The daily sedimentation rate of POC at the lagoon site was estimated using data obtained at the average depth (20 m) of the lagoon ( $6.1 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ). The calculated rate ( $73 \text{ mol C m}^{-1} \text{ d}^{-1}$ ) was equivalent to about 7% of the Pg.

At the ocean site, the vertical flux of POC in inshore and offshore zones 12 km long and 1 m wide were calculated using the data obtained at Sta. O-1 (2.5 km) and Sta. O-5 (20 km), respectively. The calculated value of  $13 \text{ mol C m}^{-1} \text{ d}^{-1}$ , obtained at 50-m depth in the inshore zone, was equivalent to 35% of the net export of POC and 1% of the Pg. The daily vertical flux of POC at 50-m depth in the offshore zone ( $7 \text{ mol C m}^{-1} \text{ d}^{-1}$ ) was equivalent to 0.7% of the Pg. The fluxes decreased with depth in each zone. In the inshore zone, about 16% of the net export of POC and 0.6% of the Pg,  $6 \text{ mol C m}^{-1} \text{ d}^{-1}$ , is transferred to a depth of 150 m below the thermocline.

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