

Organic carbon flux in Shiraho coral reef (Ishigaki Island, Japan)

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ABSTRACT: Organic carbon flux and community production rates were estimated on Shiraho coral reef (Ishigaki Island, Japan) from 19 to 26 September 1998. The daily net community production (P_n) and respiration rate (R) during the study period were 3 to 79 and 596 mmol C m⁻² d⁻¹, respectively. This resulted in a daily gross community production (P_g) of 599 to 675 mmol C m⁻² d⁻¹. The variation of P_n associated with the uncertainty of the curve fitting parameters of light response curves for photosynthesis was estimated using an error propagation formula. The averaged $P_n \pm SE$ was 36 ± 12 mmol C m⁻² d⁻¹ ($n = 23$), indicating that the P_n was significantly positive (t -test, $p < 0.05$). The apparent fluxes of dissolved organic carbon (DOC) and particulate organic carbon (POC) on the reef were estimated as 30 to 36 and 5 to 7 mmol C m⁻² d⁻¹, respectively; The sum of which was comparable with the P_n during the study period. The sediment trap study conducted at 1 km off the reef and 40 m depth showed that the vertical flux of POC was 1.0 mmol C m⁻² d⁻¹. The results indicated that 6 to 7 % of the P_g was exported to offshore and about 14 to 20 % of the POC exported from the reef flat and 0.2 % of the P_g reached 1 km off and 40 m depth.

KEY WORDS: Coral reef · Shiraho · Community production · Carbon flux · DOC · POC · Sediment trap

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INTRODUCTION

Coral reef flats and some reef communities maintain at least a 100- to 1000-fold greater biomass and a 10-fold greater areal productivity than planktonic communities of tropical oligotrophic regions that are often called the 'deserts' of the sea (Lewis 1977). The high productivity of coral reef ecosystems in a low nutrient environment has been explained by tight recycling of inorganic nutrients within the reef ecosystem (Pomeroy 1970, Johannes & Project Symbios Team 1972, Muscatine & Porter 1977). Because of a 'tight recycling system', the net organic carbon production in the system has been regarded as close to zero. Many studies, however, have estimated that such a coral reef com-

munity has excess production (e.g. Smith 1973, Atkinson & Grigg 1984, Barnes & Lazar 1994, Kayanne et al. 1995, Gattuso et al. 1996). The results indicate the importance of more precise estimation of the net organic carbon production, as well as the information on the variability of daily metabolic parameters (Gattuso et al. 1996).

Direct measurements of the fluxes of organic materials in coral reef ecosystems are also needed to confirm the estimated positive net community production. The export of organic material from some reefs to the surrounding ocean has been suggested (Quasim & Sankaranarayanan 1974, Taguchi 1982, Atkinson & Grigg 1984). However, only a few reports have shown the direct measurements of the export of organic materials in coral reef environments (Delesalle et al. 1998, Hata et al. 1998). Studies on carbon fluxes not only within coral reef areas but also between the coral reef and surrounding ocean are necessary for understand-

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ing the carbon cycle in the entire coral reef; However, so far knowledge on coral-reef ecosystems is quite limited (Erez 1990).

In this study, we estimated community production and fluxes of organic materials in a coral reef (Shiraho reef, Isigaki Island, southwest Japan) and surrounding ocean, which in earlier studies had not been carried out simultaneously. The productivity was estimated using measurements of total alkalinity (TA) and total inorganic carbon (TIC), a combination of which should give the best accuracy and precision on carbon-based estimations. A new technique to evaluate the variation of daily metabolic estimations associated with the uncertainty of the curve fitting parameters of light productivity plots is proposed. A sediment trap study was made to evaluate the vertical flux of organic materials outside the reef, as well as the direct measurement of dissolved organic carbon (DOC) and particulate organic carbon (POC) fluxes in the reef site. Using the obtained data, the daily organic carbon budget in Shiraho reef during the study period was examined.

MATERIALS AND METHODS

Study site. The studies were conducted from 19 to 26 September 1998 on Shiraho reef (24° 25' N, 124° 20' E), on the southeast coast of Ishigaki Island (Ryukyu Islands, southwest Japan; Fig. 1A). Ishigaki Island is in a monsoon area, where the prevailing wind directions are south in summer and north in winter. Shiraho reef is a fringing reef, which stretches about 1.3 km along the shore and is about 850 m wide (Fig. 1B). The geomorphology and water circulation defines the northern and southern boundary of the reef (Nakamori et al. 1991). The reef has a distinct topographical zonation from land to ocean: moat, reef pavement, reef crest and reef edge. (Iryu et al. 1995, Kayanne et al. 1995). The study site was at the middle of the reef pavement (Fig. 1B). Branched *Porites* and *Montipora*, and blue coral *Heliopora* were the dominant species of corals at the study site. A dense population of *Heliopora coerulea* in Shiraho reef is regarded as one of the world's oldest and

largest colonies. Shiraho reef was bleached in the early summer 1998 (Kayanne et al. 1999a), and the study was made during the recovery from this bleaching. The area has a semi-diurnal tidal cycle, the ranges of which are about 150 cm at spring tide and about 50 cm at neap tide. The reef crest of Shiraho is frequently exposed at low tide periods. Water on the reef flat is isolated during the low tide (the 'slack-water period') for a maximum of 5.5 h and provides suitable conditions for metabolic measurements of the reef flat community (Kinsey 1975). The water on the reef flat is flushed out during high tide. The average residence time of water on the reef flat was estimated to be about 4 to 8 h (H. Yamano unpubl. data).

Monitoring the physical variables. Wind direction and velocity were monitored using a sensor (KDC-S4)

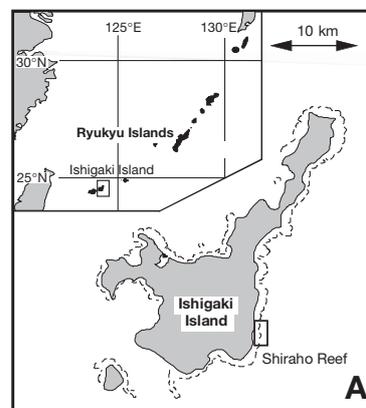
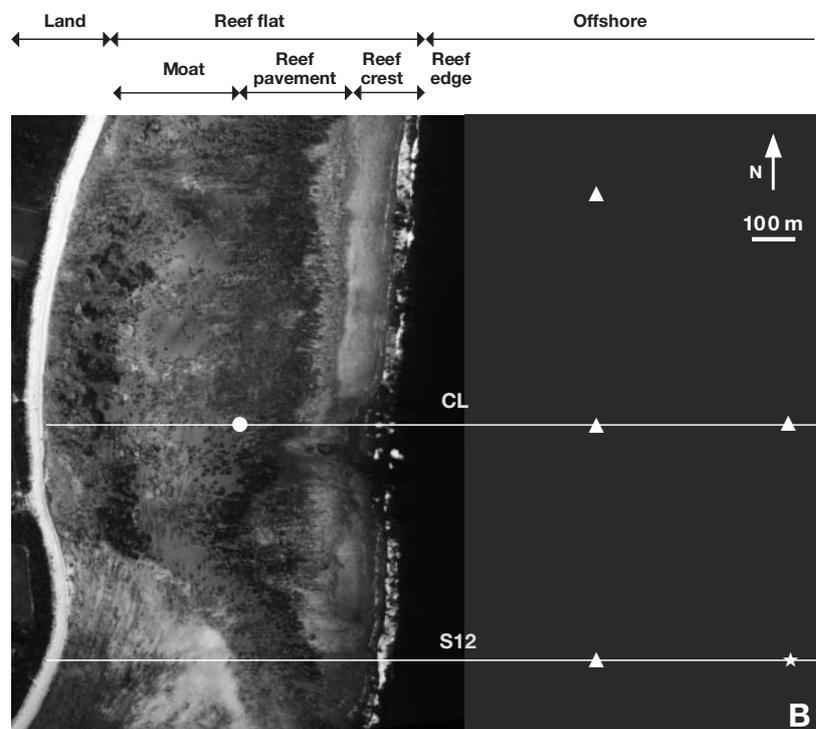


Fig. 1. (A) Location of Ishigaki Island and Shiraho reef. (B) Aerial photo of Shiraho reef on the southeast coast of Ishigaki Island. (●) study site on the reef; (▲) offshore stations; (★) station for the sediment trap study. Surface water samplings at the offshore zone were taken at 2, 4, 6 and 10 km off the reef on the transect CL, as well as at the offshore stations shown in Fig. 1B



connected to a recorder (KADEC-KAZE). Precipitation was monitored using a rain gauge (KDC-S13) connected to a recorder (KADEC-PLS; All equipment was from KONA System). The wind and precipitation were measured at the land station at about 8 m elevation 1.5 km southwest from the study point.

The water depth was measured every 15 min at the study point using a depth sensor (Argonaut-XR, Son-Tek). The beginning of the slack water period was identified by exposure of the reef crest. Most other parameters were measured using a newly developed integrated monitoring system equipped on research boat 'CREST' anchored at the study point (Kayanne et al. in press). Salinity and water temperature were monitored every minute using a water quality sensor sonde (H2O sensor, Hydrolab). The underwater irradiance was measured using a LI-192SA quantum sensor (Li-Cor) set on the sea floor, and was logged every minute to a personal computer on the boat.

Sampling procedures. Surface waters at the reef and offshore stations were sampled daily from 20 to 24 and 26 September 1998, respectively. For analyses of TA and TIC, 1 l of seawater was put into a glass bottle and was stored in the dark at 4 to 10°C until analysis within 12 h. A 250 ml seawater sample was used to measure the salinity. To measure DOC, 30 ml of seawater was filtered through a glass fiber filter (GF/F Whatman) (combusted beforehand at 550°C for 1 h) and were stored in a glass bottle at -20°C until analysis. To measure POC and particulate organic nitrogen (PON), 2 l of seawater were collected in a polyethylene container and kept in a refrigerator pending filtration within 6 hr in the field laboratory. The sample was filtered through a 25 mm GF/F and was stored at -20°C. To examine the particulate flux outside the reef, a time-series sediment trap (Model SMC7S-500, Nichiyu Giken Kogyo) was set 1 km from the reef and at 40 m depth (20 m above the bottom) from 20 to 26 September 1998 (Fig. 1B). Seven sample bottles were filled with filtered seawater containing 25 g l⁻¹ NaCl to increase the density and 2% neutralized formaldehyde, and were screwed into a rotary disc perpendicular to the funnel. When the disk rotated, 1 sample bottle moved forward and the next bottle replaced it at a set time previously programmed. Each bottle was set for 1 d, the time of which was synchronized to the tide table. The collected bottles were sealed and stored at 4°C until analysis.

Analytical procedures. In the laboratory, the TA and TIC were measured using a precision analyzer (Model EN-501A, Kimoto Electric) in conjunction with instructions from a US Department of Energy handbook (DOE 1994, Kimoto et al. 2002). The TIC data in this study was measured using a coulometer (CM5012, UIC), which was connected to the analyzer. The precision for measuring TA and TIC was 2 µmol kg⁻¹ for both vari-

ables. The salinity was measured using a salinometer (Portsal 8410A, Guildline Instruments). The DOC was measured by a high temperature catalytic oxygen method associated with a non-dispersive infrared analyzer (TOC-5000, Shimadzu). The data were calculated against standards prepared using glucose. Procedures to analyze suspended and trapped particles mostly followed Hata et al. (1998). The POC and PON in suspended and trapped particles were measured using a carbon-hydrogen-nitrogen (CHN) analyzer (MT-5, Yanaco) after HCl fume treatment to remove inorganic carbon (Yamamuro & Kayanne 1995).

Data processing. The data for specific conductance obtained by the seawater sensor sonde were converted into salinity according to the definition of UNESCO (1981), the formula of which is also detailed in Müller (1999). The calculated data were compared with the data obtained using a salinometer. Systematic error was 0.02 ± 0.01 PSU during the study period, which was corrected accordingly. Both organic and inorganic carbon production rates of the reef community were calculated from the changes in TA and TIC during the slack-water period of reef water (Smith & Key 1975).

Eqs. (1) and (2) demonstrate the calculations for the inorganic carbon production (net calcification, g_n) rate and organic carbon production (net photosynthesis, p_n) rate, respectively:

$$g_n(\text{mmol C m}^{-2} \text{ h}^{-1}) = -\frac{d\text{TA}}{2} \times \rho \times D \times t^{-1} \times 10^{-3} \quad (1)$$

$$p_n(\text{mmol C m}^{-2} \text{ h}^{-1}) = -\left(d\text{TIC} - \frac{d\text{TA}}{2}\right) \times \rho \times D \times t^{-1} \times 10^{-3} \quad (2)$$

where dTA is change in total alkalinity (µmol kg⁻¹), dTIC is change in total inorganic carbon (µmol kg⁻¹), ρ is seawater density (kg m⁻³) as, given by Millero & Pissin (1981), D is water depth (m) averaged for a 50 × 50 m range around the study site based on relative height data of 25 grids. and t is duration (h⁻¹).

The respiration rate (r) was obtained by p_n measured at night. The gross community production rate (p_g) was given by the sum of p_n and $|r|$.

The rates of p_n and g_n were plotted against the light intensity. The hyperbolic tangent function (tanh) was used to obtain light-saturation curves of photosynthesis and calcification as recommended by Chalker (1981):

$$p_n = p_{\text{max}} \times \tanh(i/I_k) + r \quad (3)$$

where p_{max} is the maximum photosynthesis rate, I_k is the constant determined by the initial slope and p_{max} (Chalker 1981), r is the respiration rate (see above), and i is light intensity, when the curve was fitted for the calcification, $p_n = g_n$, $p_{\text{max}} = g_{\text{max}}$ and $r = g_n$ at night. The curve fitting was computed using SYSTAT 5 running on

a Macintosh computer. Daily production rates were calculated by integrating the production rates with daily light intensity. Gattuso et al. (1996) pointed out that simulated light data (e.g. a sine curve) grossly overestimates the daily average daily irradiance. The data was processed using light data collected at the site for every min in order to avoid such an overestimation. The daily net community production (P_n), daily community respiration rate (R), gross community production (P_g) and net community calcification (G_n) were obtained by integration for p_n , lr , p_g and g_n for 24 h, respectively.

Evaluation of the error of daily production estimates. To evaluate the variation of the daily metabolic estimations associated with the uncertainty of the curve fitting parameters, we used the general formula of error propagation (Taylor 1982). For convenience, the hyperbolic function (Eq. 3) is expressed in the following:

$$\begin{aligned} p &= f(x, y, z) \\ &= x \times \tanh(i/y) + z \\ &= x \times \frac{e^{2i/y} - 1}{e^{2i/y} + 1} + z \end{aligned} \quad (4)$$

The ' i ' represents light intensity, which is treated as a constant in the equation. The standard deviation (SD) of ' p ' (σ_p) at a fixed light intensity (i) derived from the error of x , y and z can be calculated as follows:

$$\begin{aligned} \sigma_p^2 &= \left(\frac{\partial p}{\partial x}\right)^2 \sigma_x^2 + \left(\frac{\partial p}{\partial y}\right)^2 \sigma_y^2 + \left(\frac{\partial p}{\partial z}\right)^2 \sigma_z^2 \\ &+ 2 \frac{\partial p}{\partial x} \frac{\partial p}{\partial y} \sigma_{xy} + 2 \frac{\partial p}{\partial x} \frac{\partial p}{\partial z} \sigma_{xz} + 2 \frac{\partial p}{\partial y} \frac{\partial p}{\partial z} \sigma_{yz} \end{aligned} \quad (5)$$

σ_x^2 , σ_y^2 and σ_z^2 represent the variances of x , y and z , respectively. The σ_{xy} , σ_{yz} and σ_{zx} represent covariances between x , y and z . If the errors of x , y and z are random and independent of each other, then all covariances equal 0; However this is not the case in the hyperbolic tangent function. The $\partial p/\partial x$, $\partial p/\partial y$ and $\partial p/\partial z$ represent the partial derivatives for x , y and z , respectively, as follows:

$$\begin{aligned} \frac{\partial p}{\partial x} &= \tanh(i/y) \\ \frac{\partial p}{\partial y} &= -\frac{4ie^{2i/y}}{y^2 \times (e^{2i/y} + 1)} \times x \\ \frac{\partial p}{\partial z} &= 1 \end{aligned} \quad (6)$$

To obtain the SD of the P_n , which is integrated against irradiance data, Eq. (5) should be converted as follows:

$$\begin{aligned} \sigma_{P_n}^2 &= \left(\sum \frac{\partial p}{\partial x} \Delta t\right)^2 \sigma_x^2 + \left(\sum \frac{\partial p}{\partial y} \Delta t\right)^2 \sigma_y^2 + \left(\sum \frac{\partial p}{\partial z} \Delta t\right)^2 \sigma_z^2 \\ &+ 2 \left(\sum \frac{\partial p}{\partial x} \Delta t\right) \left(\sum \frac{\partial p}{\partial y} \Delta t\right) \sigma_{xy} + 2 \left(\sum \frac{\partial p}{\partial x} \Delta t\right) \\ &\times \left(\sum \frac{\partial p}{\partial z} \Delta t\right) \sigma_{xz} + 2 \left(\sum \frac{\partial p}{\partial y} \Delta t\right) \left(\sum \frac{\partial p}{\partial z} \Delta t\right) \sigma_{yz} \end{aligned} \quad (7)$$

where Δt is the interval for integrated data (1 min).

The SD of the mean (SDOM: $\sigma_{\bar{P}_n}$), which is often expressed as standard error (SE), is given by:

$$\sigma_{\bar{P}_n} = \sigma_{P_n} / \sqrt{N} \quad (8)$$

N is the number of the data.

The variances and covariances of the curve fitting parameters were calculated using an N-88 BASIC program for least-square method (KOTARO, Sankaido) programmed after Sato (1997).

RESULTS AND DISCUSSION

Environmental conditions

The underwater light intensity was $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 12:00 h (Fig. 2a), which was about 50 to 60% of that in air found during the study period. The water depth measurements indicated that the slack water period started at a depth below 155 cm and ended with a rise of water level (Fig. 2c). The water temperature was 28 to 30°C, and the maximum and minimum temperatures were at the end of the slackwater period during the day and night, respectively. Reef water salinity was 34.4 to 34.8 PSU, which increased during the day slack water period because of evaporation and decreased after precipitation (Fig. 2b,e). A salinity decrease caused by inflow of river water and underground water did not occur at the study point during the study period. The concentrations of inorganic nitrogen ($\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) and phosphorus (PO_4^{3-}) during the study periods were about 1 to 2 and 0.01 to 0.04 μM , respectively (T. Miyajima unpubl. data).

Daily production rates

The TA and TIC in the reef water were 2150–2295 and 1570–2085 $\mu\text{mol kg}^{-1}$, respectively, and in the off-shore water were 2263–2270 and 1915–1922 $\mu\text{mol kg}^{-1}$, respectively. The TA and TIC decreased during the day and increased during the night. This was due to photosynthesis (TIC decrease) and calcification (TIC and TA decrease) during the day and respiration (TIC increase) during the night. The rates of calcification and photosynthesis calculated by Eqs. (1) and (2) were

plotted against light intensity (Fig. 3). Curve fitting parameters for calcification and photosynthesis simulated by the hyperbolic tangent function (Eq. 3) were obtained by the resulting curves. Daily production rates were calculated by integrating the production curves with daily light intensity (Table 1). The P_n was 3 to 79, at an average of $36 \text{ mmolC m}^{-2} \text{ d}^{-1}$. R was

$596 \text{ mmolC m}^{-2} \text{ d}^{-1}$. Thus resulted in P_g of 599 to $675 \text{ mmolC m}^{-2} \text{ d}^{-1}$. G_n was almost constant at an average of $127 \text{ mmolC m}^{-2} \text{ d}^{-1}$. The data were revised from the report by Kayanne et al. (1999b), by reconsidering the water depth data (see 'Materials and methods'). Several studies have been made of the community metabolism of Shiraho reef. (Nakamori et al. 1991, Suzuki et

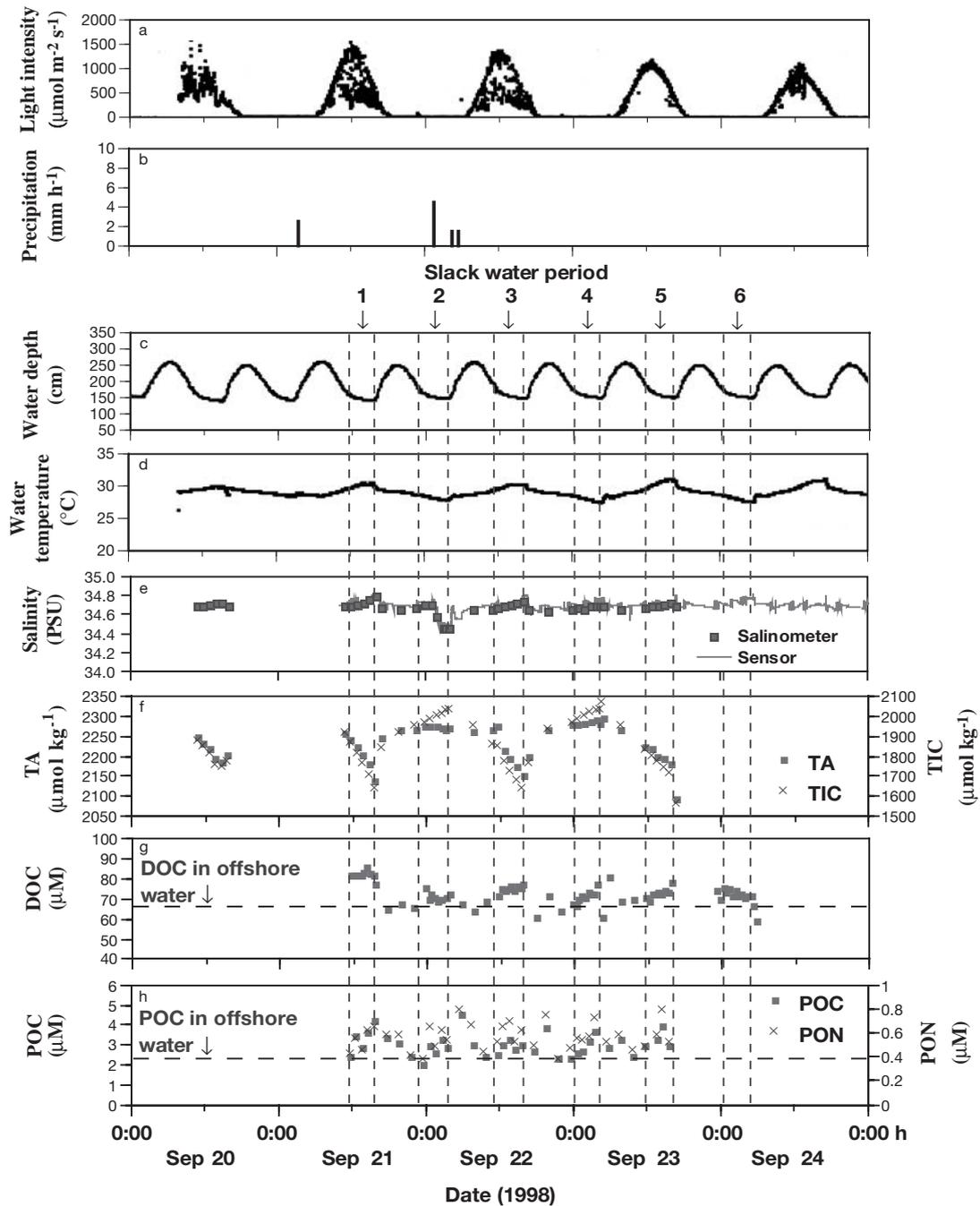


Fig. 2. Time series of physical and chemical parameters in seawater on the Shiraho reef flat from 20 to 24, September 1998. TA: total alkalinity; TIC: total inorganic carbon; DOC: dissolved organic carbon; POC: particulate organic carbon; and PON: particulate organic nitrogen

Table 1. Daily community production rates of Shiraho reef during the study period (21 to 24 September 98). I is daily integrated irradiance, P_g is daily gross community production, R is daily community respiration rate, P_n is daily net community production and G_n is net daily community calcification

Date (1998)	I (mol m ⁻² d ⁻¹)	P_g	R (mmol C m ⁻² d ⁻¹)	P_n	G_n
21 Sep	22	622	-596	26	128
22 Sep	21	599	-596	3	127
23 Sep	24	675	-596	79	126
24 Sep	20	631	-596	36	128
Daily average	22	632	-596	36 ± 12 ^a	127

^aEstimated SE associated with the uncertainty of the curve fitting parameters (see text)

al. 1995). The P_g of coral communities on Shiraho reef in September 1990 was 412 to 460 mmol C m⁻² d⁻¹. The community metabolism at the same point as this study was 434 mmol C m⁻² d⁻¹ in March 1993 (Kayanne et al. 1995). The range of the reported data is attributable to spatial and seasonal variation; However, the P_n of the study period (36 mmol C m⁻² d⁻¹) was at a lower limit than found in previous studies (26 to 110 mmol C m⁻² d⁻¹). The lower P_n can be explained by the lower coverage of corals because of a bleaching event (H. Kayanne et al. unpubl. data). During the study period (September 98), the coverage of corals was 7.1% with 50% bleaching. Therefore, the coverage of healthy corals was 3.6% (half of 7.1%). The bleached corals were also still alive and they played a role as consumers in the ecosystem and this in turn lowered P_n

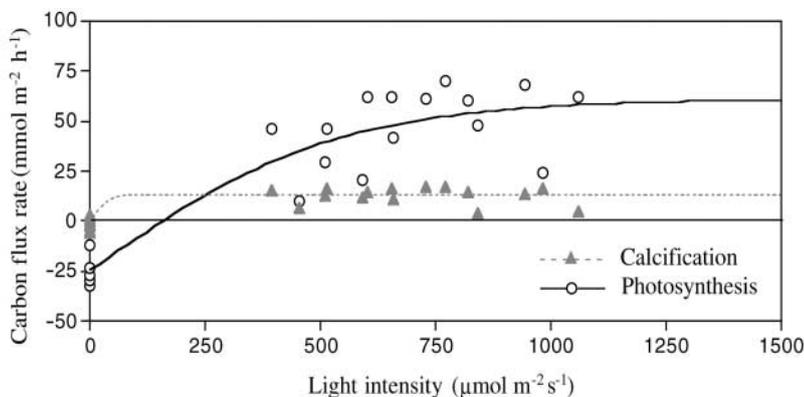


Fig. 3. Light response curves for photosynthesis and calcification. The fitting equation is hyperbolic tangent function (see text). The curve fitting parameters (mean ± SE) for photosynthesis and calcification are: Photosynthesis (mmol m⁻² h⁻¹): $p_{max} = 86 ± 2$, $I_k = 526 ± 36$, $r = 25 ± 1$ ($r^2 = 0.872$). Calcification (mmol m⁻² h⁻¹): $g_{max} = 15 ± 0.4$, $I_k = 35 ± 44$, g_n at night = $2 ± 0.3$ ($r^2 = 0.771$). The curve fitting parameters were calculated by SYSTAT 5 running on a Macintosh computer. The N-88 BASIC program (KOTARO, Sankaido), that was programmed after Sato (1997), calculated the SEs of the curve fitting parameters

during the study period. The productivity measured 1 yr later (September 99), when the coverage recovered to 6.7%, showed that P_n was 113 mmol C m⁻² d⁻¹.

Error analysis of daily production rate

The ratio of gross photosynthesis to respiration (P_g/R) was $1.06 ± 0.03$ ($n = 4$), indicating that the reef system was autotrophic. The SE of the P_n associated with the uncertainty of the curve fitting parameters (estimated by Eq. 7) was 12 mmol C m⁻² d⁻¹. The data ($36 ± 12$ mmol C m⁻² d⁻¹; $n = 23$) indicated that the P_n was significantly positive (t -test, $p < 0.05$) during the study period. Gattuso et al. (1996) pointed out the importance of evaluating the uncertainty of estimated daily metabolic parameters and proposed a Monte Carlo simulation method. The Monte Carlo method, however, is a numeric experimental which provides a solution as a rough approximation (Miyatake & Wakimoto 1978). In this report, we introduced the theoretical and statistical method. We computed a propagated error derived from the asymptotic SEs of curve fitting parameters (Eq. 5). An integrated form of propagation of error (Eq. 7) was a new formula to obtain the confidence interval in the daily metabolic parameters, which provided the best estimator.

Concentrations and fluxes of DOC and POC on the reef

This report is the first to study the concentrations and fluxes of DOC and POC in seawater on Shiraho reef. The concentrations of DOC (60 to 87 μM, average 72), POC (2.0 to 4.5 μM, average 3.1) and PON (0.39 to 0.81 μM, average 0.57) were lower compared with the data reported for other reef sites, reviewed by Sorokin (1993) and Torron et al. (1997); this is mainly attributable to the shorter residence time (4 to 8 h) of the water in the study area. The lower P_n during the study period discussed above might relate to lower concentrations of DOC and POC, but it remains to be studied. The concentrations of DOC, POC and PON in offshore water (average ± SE) were $68 ± 3$ ($n = 5$), $2.3 ± 0.2$ ($n = 10$) and $0.45 ± 0.02$ ($n = 10$) μM, respectively. The concentrations of DOC, POC and PON were higher in reef water during the slack water period than those in offshore water both during the day and night, and were returned to the offshore value during the high tide period (Fig. 2). Such diurnal patterns suggested an input of organic materials into ambient water on the reef flat and the net export of organic mate-

rials from the reef to offshore. The results were consistent with the positive P_n .

Two types of estimation for the fluxes of DOC and POC were made. First, the rates of the changes in DOC and POC during slack water periods were calculated by a regression analysis (Table 2, Fig. 4). The slope of the regression ($\mu\text{mol l}^{-1} \text{h}^{-1}$) was considered a net flux during the periods. To estimate the daily fluxes of DOC

and POC on the reef, the calculated fluxes of DOC and POC during the slack water period was integrated for each 12 h period of the day and night. The averaged DOC and POC fluxes were 30 and 5 $\text{mmolC m}^{-2} \text{d}^{-1}$, respectively. The changes in the concentrations of DOC were sometimes negative, though they were not significant (Table 2). We suppose that the apparent negative flux of DOC occurred by the occasional larger

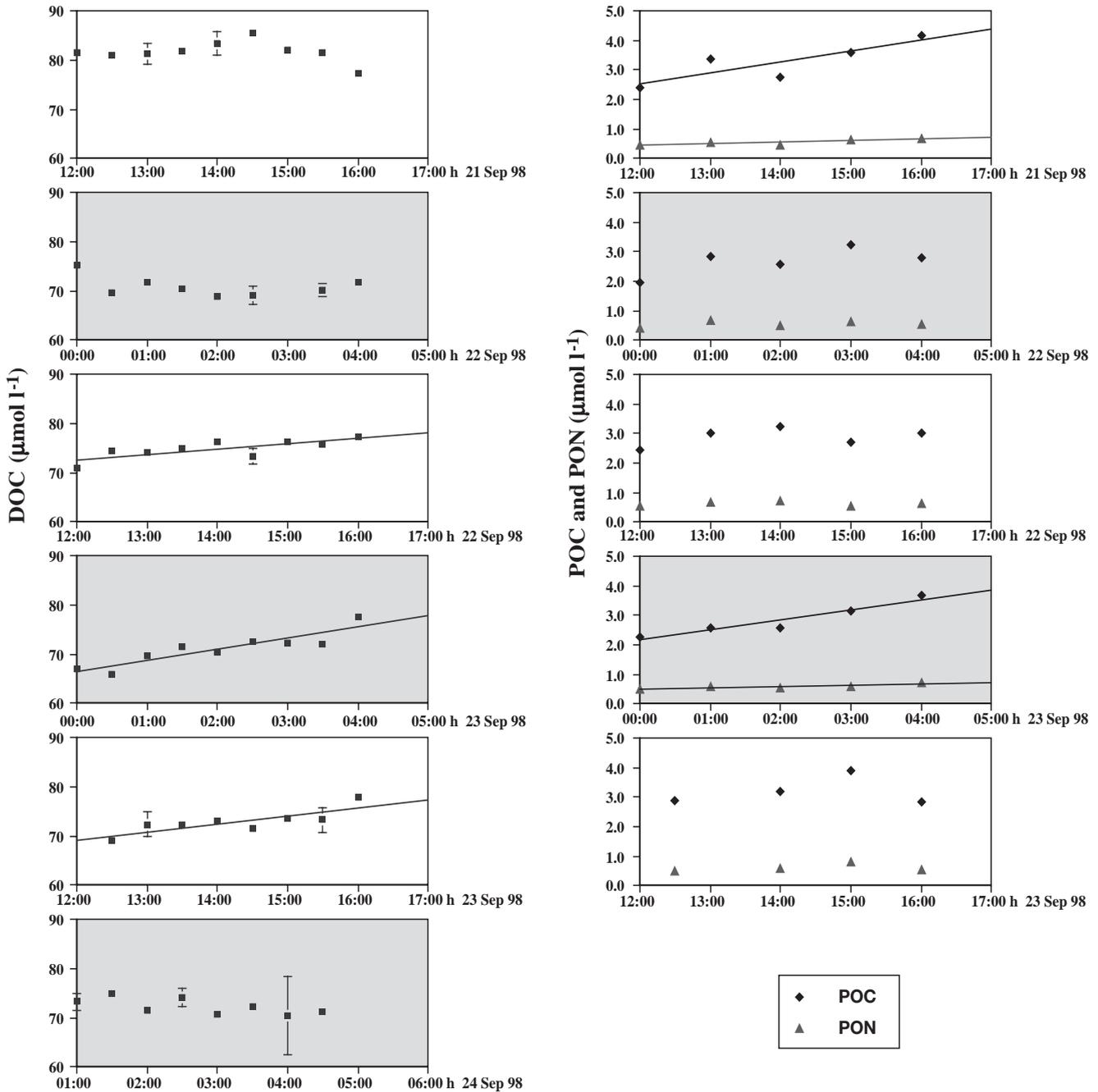


Fig. 4. Changes in the concentrations of DOC, POC and PON during slack-water periods on the Shiraho reef flat (21 to 24 September 1998). The shaded frames are data at night (00:00 to 05:00 h, except 24 September with data from 01:00 to 06:00 h), unshaded frames are data in the day (12:00 to 17:00h)

Table 2. Estimations of organic carbon flux in Shiraho reef (21 to 24 September 1998). ns: not significant, the net flux being regarded as 0; nm: not measured. Averaged water depth of 151 cm during the slack water period was used in the calculation of integrated flux. * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$

Date (1998)	DOC			POC		
	Number of the data	Rate \pm SE ($\mu\text{mol l}^{-1} \text{h}^{-1}$)	Integrated flux for 12 h (mmol m^{-2})	Number of the data	Rate \pm SE ($\mu\text{mol l}^{-1} \text{h}^{-1}$)	Integrated flux for 12 h (mmol m^{-2})
21 Sep (day)	9	-0.4 ± 0.8	ns	5	$0.37 \pm 0.13^*$	6.6
22 Sep (night)	8	-0.6 ± 0.6	ns	5	0.21 ± 0.13	ns
22 Sep (day)	9	$1.1 \pm 0.3^{**}$	20	5	0.09 ± 0.10	ns
23 Sep (night)	9	$2.2 \pm 0.4^{***}$	41	5	$0.33 \pm 0.06^{***}$	6.1
23 Sep (day)	8	$1.6 \pm 0.5^{***}$	29	4	0.07 ± 0.19	ns
24 Sep (night)	8	-0.9 ± 0.4	ns	nm		
Total			90			12.7
Daily average			30			5.1

heterotrophic consumption of DOC than excretion of DOC by primary producers (discussed in the following section). Second, the fluxes of DOC and POC were calculated by the difference in the concentrations of DOC and POC in reef water and offshore water and the residence time of reefwater:

$$\text{Flux (mmol m}^{-2} \text{d}^{-1}) = ([\text{OC in reef water}] - [\text{OC in offshore water}]) \times D/T$$

where OC is concentration of organic carbon ($\mu\text{M} = \text{mmol m}^{-3}$), D is average water depth (m) and T is residence time of reef water (d).

In the estimation here, residence time was set at 6 h (= 0.25 d) (see description in 'Materials and methods'). Using the equation, the fluxes of DOC and POC were estimated at 36 and 7 $\text{mmol C m}^{-2} \text{d}^{-1}$, respectively. The values were comparable with that of the previous reports, although little information is available on DOC and POC flux in coral reefs and other coastal aquatic ecosystems. Ikeda et al. (1995) measured the concentrations of DOC and POC in seawater flowing across the reef flat of Palau (western Pacific) and estimated the daily flux as 64 $\text{mmol C m}^{-2} \text{d}^{-1}$. Ziegler & Benner (1999) estimated the DOC flux in a subtropical seagrass-dominated lagoon (Laguna Madre, Texas) as 4 to 25 $\text{mmol C m}^{-2} \text{d}^{-1}$. As for POC flux, Johannes (1967) reported that the flux of particulate organic materials (POM) on the reef flat of Enewetok atoll (Marshall Islands) is 200 $\text{mg m}^{-2} \text{h}^{-1}$. If we assume that POM has a 40% carbon content and the POM flux rate is constant throughout the day, the data can be converted to 20 $\text{mmol C m}^{-2} \text{d}^{-1}$.

Production and consumption of organic carbon in reef water

One of the main sources of organic carbon in seawater on the reef flat is attributable to a release of organic materials by coral (Marshall 1965, Coles & Strathmann 1973). Symbiotic algae (zooxanthellae) in a host coral ex-

crete 80 to 95% of the photosynthetically fixed carbon to the coral (Davies 1984, Muscatine et al. 1984, Edmond & Davies 1986). The coral respire some part of the organic carbon and secrete the rest into the surrounding waters, which is about 6 to 48% of photosynthetically fixed carbon (Crossland et al. 1980, Davies, 1984, Muscatine et al. 1984, Edmond & Davies 1986). Coral mucus consists of neutral sugars, amino sugars, proteins, phospholipids, triglycerides, sterols and wax esters (Benson & Muscatine 1974, Ducklow & Mitchell 1979, Crossland 1987), which can be used as a food source for bacteria which are considered as a main consumer of DOM and POM in seawater (Moriarty et al. 1985a, Ducklow 1990). Stimulation of bacterial growth by the coral mucus has been observed (Paul et al. 1986, Schiller & Hendl 1989, Gast et al. 1998), but the quantitative importance of degradation of DOC and POC in carbon flux is difficult to assess as it depends on: (1) The mucus production rate; (2) The degradation rate in ambient conditions; and (3) The carbon conversion efficiency of bacteria on mucus (Torreton 1998). Bacterial production reported over coral reef waters show a wide range from 0.02 to 147 $\mu\text{g C l}^{-1} \text{d}^{-1}$ (Moriarty et al. 1985b, Liney & Koop 1986, Sorokin 1994, Torreton et al. 1997, Ferrier-Pages & Gattuso 1998). In Shiraho reef, the bacterial production in the water column was estimated to be 20 to 30 $\mu\text{g C l}^{-1} \text{d}^{-1}$ (A. Watanabe unpubl. data), but the data in the sediments is not available at present. Very few data have been reported for the bacterial production in the reef sediments; Those that have ranged from 20 to 370 $\text{mg C m}^{-2} \text{d}^{-1}$ with around an average of 130 $\text{mg C m}^{-2} \text{d}^{-1}$ (Moriarty et al. 1985b, Moriarty & Hansen 1990, Hansen et al. 1992). With the data available, we have primarily assumed the bacterial production rate in water and sediments on Shiraho reef as 25 $\mu\text{g C (2 } \mu\text{mol) l}^{-1} \text{d}^{-1}$ and 130 $\text{mg C (11 mmol) m}^{-2} \text{d}^{-1}$, respectively. The areal bacterial production rate was estimated to be 15 $\text{mmol C m}^{-2} \text{d}^{-1}$, with an average water depth of 2 m in Shiraho reef. As for carbon conversion efficiency, a value of 50% (Ducklow 1983) has frequently been adopted in calculations of car-

bon budgets in the previous studies (Moriarty et al. 1985b, Moriarty & Hansen 1990, Hansen et al. 1992). However, lower values (7 to 20 %) have been observed in oligotrophic regions (Bjørnsen 1986, Hendl & Velimirov 1986, Torretton 1999). When we adopted the conversion efficiency of 20 and 50 %, the bacterial consumption of DOC + POC were estimated as 75 and 30 $\text{mmol C m}^{-2} \text{d}^{-1}$, respectively.

Vertical flux of POC outside the reef

Fig. 5 shows the time series of the vertical fluxes of POC and PON at a depth of 40 m at 1 km from the reef. Vertical fluxes of POC and PON (average \pm SE) were 1.03 ± 0.07 and 0.11 ± 0.01 $\text{mmol m}^{-2} \text{d}^{-1}$, respectively (Fig. 5, Table 3). A sediment trap is one method used to evaluate the flux of POM, but the data are quite limited outside the reef areas (Delesalle et al. 1998, Hata et al. 1998). The POC flux of this study was comparable with that in Palau reef under similar conditions (Hata et al. 1998), but the reported data for Tiahura reef (Moorea Island, French Polynesia) (Delesalle et al. 1998) was lower ($0.20 \text{ mmol C m}^{-2} \text{d}^{-1}$ at 30 m depth and 10 m above the bottom) (Table 3). The sedimentation rates obtained in the coral reef lagoons show a wide range from 73 to 3900 $\text{mg}(6 \text{ to } 325 \text{ mmol})\text{C m}^{-2} \text{d}^{-1}$ (Koop & Larkum 1987, Charphy & Charpy-Roubaud 1991, Hansen et al. 1992, Clavier et al. 1995, Hata et al. 1998), but were higher than those outside the reef.

The daily sedimentation rate of POC outside the reef was compared to the daily areal POC flux on the reef. Because of the short residence time of seawater on the Shiraho reef (4 to 8 h), we can assume that most of the POC in seawater which is released on the reef flat is subsequently exported to offshore. The vertical flux of POC outside the reef ($1.0 \text{ mmol C m}^{-2} \text{d}^{-1}$) was 14 to 20 % of the POC flux on the reef ($5 \text{ to } 7 \text{ mmol C m}^{-2} \text{d}^{-1}$), indicating that more than 80 % of POC was decomposed during sedimentation outside the reef. The similar

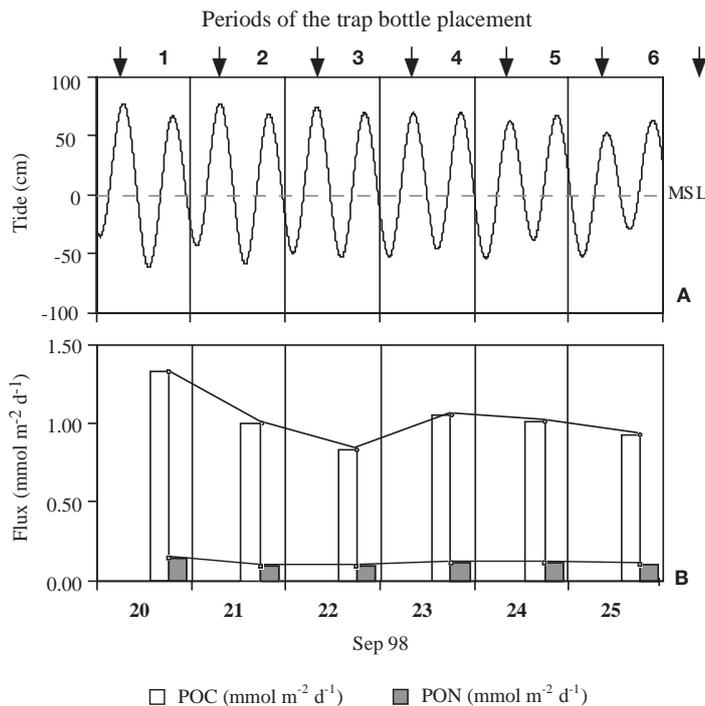


Fig. 5. (A) Time series of the tide offshore. (B) Vertical fluxes of POC and PON at 40 m depth at 1 km off the reef. MSL: mean sea level

Table 3. Sedimentation rates outside the coral reef (mean \pm SE). -: not reported

Study site	Study period	Distance from reef edge (km)	Sampling maximum depths (m)	POC in surface water (μM)	POC flux	PON flux	Molar C/N ratio	Source
Shiraho (Ishigaki Island, Japan)	Sep 98	1	40 (60)	2.3	1.03 ± 0.07 (n = 6)	0.11 ± 0.01	9.6	This study
Palau (Western Pacific)	Aug 95	2.5	50 (>700) 150 (>700) 300 (>700)	3.8	1.08 ± 0.28^a 0.53 ± 0.11^a 0.40 ± 0.02^a	0.15 ± 0.03^a 0.07 ± 0.01^a 0.03 ± 0.00^a	7.2 7.6 13.3	Hata et al. (1998)
Tiahura (Moorea Island, French Polynesia)	Sep 93	-	ca. 38 (40) 30 (40) 420 (430)	2.7 ^c	4.69 ± 0.50^b 0.20 ± 0.02^b 0.37 ± 0.06^b		9	Delasalle et al. (1998)

^aSE was calculated from the originally reported data for SD
^bData was converted from mg l^{-1} in the reported data
^cData was converted from mg l^{-1} in the reported data

result was reported by Hata et al. (1998), the sedimentation rate outside the coral reef in Palau at 50 m depth was 35% of export POC. We also examined the relationships between day-to-day variations of the sedimentation rates outside the reef and the variations of the P_n , and the concentrations and fluxes of DOC and POC, but the relationship was not clear. Further information is needed to characterize the sedimentation pattern outside the reef, such as a long-term study including information on hydrodynamics.

Composition of organic materials

The C/N ratios of organic particles may give some insight into their origins. The C/N ratios of some potential sources of particulate materials have been reported: Phytoplankton (6 to 8: Parsons et al. 1961), benthic marine plant (20: Atkinson & Smith 1983), coral mucus (6.9 to 13.7: Johannes 1967), mucous sheet of coral (4.8 to 5.9: Cofforth 1990) and terrestrial vascular plant (>30: Alexander 1977). According to the molar C/N ratio of particulate materials obtained in this study (5.5 ± 0.3 ; $n = 37$), we suppose that the organic particles in the Shiraho reef mainly originate from mucus and mucous sheet of corals and that the effect of vascular plants is small. The concentrations of chlorophyll *a* (chl *a*) in the water was $0.15 \pm 0.01 \mu\text{g l}^{-1}$ ($n = 37$). Assuming that the C/chl *a* ratio = 30 (Banse 1977), the contributions of phytoplankton biomass to the POC was estimated to be 12%.

The C/N ratio of the trapped particles outside the reef was 9.6, which was greater than that of reef water (5.5) or POM in the surface water in offshore zone (5.1 ± 0.3 ; $n = 10$), suggesting the loss of nitrogen during the sedimentation. One other important aspect is the identification of the organic materials collected outside the reef in order to show the origin of the materials. It is important to evaluate the contribution of the reef organisms on the sinking particles collected outside the reef, but we have little information at present. The ratios of carbon to nitrogen or chl *a* (Hata et al. 1998) and the content of carbohydrates, amino acids and sugars (Delasalle et al. 1998) have been reported. However, the data for fatty acid compositions or stable isotope values are much more informative to identify the origin of the organic materials, which is a study required for the near future.

Organic carbon budget in Shiraho reef

The daily carbon budget in Shiraho reef during the study period was examined (Table 4) and the data obtained was assumed to be representative of the study area.

It was suggested that inshore corals derive much of their nutrients from terrestrial sources (Risk et al. 1994); However, no depletion in salinity by freshwater input and lower C/N ratio of particulate materials (discussed above) indicated that the effect of terrestrial materials on POC and DOC fluxes was negligible during the study period.

Primary producers on the reef flat fixed carbon at the rate of $632 \text{ mmolC m}^{-2} \text{ d}^{-1}$. Although most of this fixed carbon was consumed by community respiration ($596 \text{ mmolC m}^{-2} \text{ d}^{-1}$), a large amount of the fixed carbon was left as P_n ($36 \pm 12 \text{ mmolC m}^{-2} \text{ d}^{-1}$). The apparent flux of DOC + POC was estimated to be 35 to $43 \text{ mmolC m}^{-2} \text{ d}^{-1}$, which was 6 to 7% of P_g and almost equivalent to P_n during the study period. The heterotrophic consumption of organic carbon by bacterial activity, 30 to $75 \text{ mmolC m}^{-2} \text{ d}^{-1}$, was assumed from the data available from the previous reports. With the numbers estimated, the release of POC + DOC from the primary producers were estimated to be 69 to $114 \text{ mmolC m}^{-2} \text{ d}^{-1}$, which was 11 to 18% of the P_g . The bacterial consumption of DOC + POC was assumed to be about 43 to 66% of DOC + POC production by the primary producers during the study period. Because of the short residence time of seawater on the Shiraho reef (4 to 8 h: H. Yamano unpubl. data), most of the organic materials remained in seawater on the reef flat and was subsequently exported to offshore. With POC, the sediment trap study indicated that $1 \text{ mmolC m}^{-2} \text{ d}^{-1}$, which is equivalent to about 14 to 20% of the POC exported

Table 4. Daily carbon budget in Shiraho coral reef (21 to 24 September 1998)

	Method	Flux ($\text{mmolC m}^{-2} \text{ d}^{-1}$)	% of P_g
Gross community production (P_g)	Measurement of TA and TIC	632	100
Daily community respiration (R)		596	94
Daily net community production (P_n)		36 ± 12	6
Net community calcification (G_n)		127	–
Apparent flux of DOC on the reef	HTCO method	30–36	5–6
Apparent flux of POC on the reef	CHN analyzer	5–7	1
Bacterial heterotrophic consumption of DOC + POC on the reef	Estimated from the reported data	30–75	5–12
Excretion of DOC + POC by primary producers	Calculated	69–114	11–18
Vertical flux of POC outside the reef (1 km off reef and 40 m depth)	Sediment trap + CHN analyzer	1	0.2

from the reef flat (5 to 7 mmol C m⁻² d⁻¹) and 0.2 % of the P_g , reached 1 km off the reef and 40 m depth. Although all the values have uncertainties, we showed that the flux of DOC and POC in Shiraho reef was in good accordance with the estimated community production during the study period.

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