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Phosphorus metabolism in coral reef communities: exchange between the water column and bottom biotopes

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Abstract

Exchange of phosphate between components of the reef bottom and the water column were studied on reefs around Heron Island (Great Barrier Reef), both in aquaria and in *in situ* enclosures, using radioactive phosphorus (^{32}P) as a tracer. Living corals, dead corals, coral rubble overgrown with periphyton, and soft sediments of coral sand were used in experiments. In all of these components of bottom reef biotopes, two opposite flows of inorganic phosphate were recorded and measured, i.e. the rate of PO_4-P uptake from water (A_c), and its release (A_e). At ambient PO_4-P concentrations in water of 0.1–0.3 μmol l^{-1}, both flows varied in living corals and coral rubble between 10 and 70 μg P kg^{-1} h^{-1}, 3–10 mg P m^{-2} day^{-1}, and in coral sand between 10 and 30 μg P kg^{-1} h^{-1}, or 2–7 mg P m^{-2} day^{-1}. Under the latter concentration range (which is typical for coral reef areas), the reciprocal PO_4-P flows almost balanced each other, so that net uptake (A_t) was very low. Often it approached zero or was positive, showing that a net PO_4-P release had taken place. The uptake flow (A_c) in living coral was much more dependent on the PO_4-P content in overlying water than was the release flow (A_e). The influence of conditions of illumination upon the values of A_c and A_e was comparatively low. The data obtained are used to discuss problems of phosphorus balance and dynamics in coral reef ecosystems.

Introduction

Autotrophic communities of reef benthic biotopes function effectively at very low concentrations of the limiting inorganic nutrients nitrogen and phosphorus (Crossland, 1983). The photosynthetic production, being at a level of 2–6 g C m^{-2} day^{-1}, appears to be uncorrelated to ambient nutrient concentrations in surrounding waters (Kinsey, 1977, 1983; Wiebe, 1985; Sorokin, 1990). This high production can be sustained largely by high turnover rates of nutrients in the water-substrate system and within the benthic biotopes themselves (Atkinson, 1987). Earlier attempts to quantify these high turnover rates have failed. Measurement of their dynamics in oceanic waters crossing rich reef-flat biotopes (Johannes *et al.*, 1972; Webb *et al.*, 1975; Atkinson, 1983; Crossland & Barnes, 1983; Hatcher, 1985), as well as estimation of nutrient dynamics by measurement of changes in their ambient concentrations within *in situ* plastic enclosures on the bottom (Henderson, 1981; Propp *et al.*, 1983) showed only a weak and indefinitely directed flow between the substrate and the water column. Sometimes this flow was from the water to the bottom, sometimes in the opposite direction. In most experiments, bottom reef biotopes have been

found to release some nitrogen (as a consequence of nitrogen fixation) and to consume some phosphorus, but in amounts that are an order or more less than would be expected from the metabolic rates (Atkinson, 1983). Sometimes, instead of consumption, a net release of phosphate has been found (Andrews & Miller, 1983; Propp *et al.*, 1983).

The ambiguous assessment of phosphorus exchange obtained by using the above approaches can also be exemplified by the findings of Propp *et al.* (1983), who used enclosure techniques. In their experiments, the concentrations of inorganic N and P in water over a bottom covered with coral rubble or coral sand actually changed little during time in the dark or the light. Usually it was stable over time, or there was a weak release not only of N (which is understandable because of possible N_2 fixation) but also of P (which is supposed to be consumed by autotrophs in light rather than being released) (Atkinson, 1983). Similar data were obtained by Henderson (1981). It is obvious that coral rubble and coral sand contain actively functioning autotrophic and heterotrophic components growing within periphyton or on coral sand particles (Sorokin, 1981). These might consume and release inorganic N and P simultaneously, creating two opposite flows that actually should not depend much on light, since autotrophs also actively consume nutrients in the dark (Sorokin, 1985). Thus, measurement of changes in ambient concentrations in space (along the flow of water) or in time (in enclosures) cannot in principle be related to the uptake and release of PO_4-P, but rather to the balance between them. The level of this balance could be low or zero when the rates of both flows are in equilibrium.

A possible method for evaluating the real values of these nutrient flows between bottom biotopes and the water column lies in the use of labelled isotopic nutrients (^{15}N, ^{32}P or ^{33}P) together with net exchange estimations (Pomeroy *et al.*, 1974; D'Elia, 1977; Atkinson, 1981, 1981a, 1987; Burris, 1983). By using these methods to measure any decrease in the concentration of labelled inorganic nutrient in enclosed water over a bottom biotope, the real flow of the nutrient from the water into the bottom biotope can be evaluated. It cannot be masked by the opposite flow of the same nutrient from the bottom biotope into the water because the bottom biotope does not contain the labelled isotope. This approach we have used to measure the exchange rates of phosphate between the water column and the components of bottom biotopes on reefs off Heron Island, Great Barrier Reef.

Methods

Experiments with living corals, dead coral rubble, dead coral colonies, pieces of flat rock covered with periphyton, and coral sands were conducted both in aquaria and (with the sands) within *in situ* enclosures. Estimates were made of the absolute rates of uptake (A_c) and release (A_e) of inorganic phosphates by the above components. The values of A_c and A_e were expressed as $\mu g\ P\ kg^{-1}$ (dry weight) h^{-1}. The uptake rate (A_c) was measured with the use of labelled phosphate, PO_4-^{32}P. Aliquots (1 ml) of labelled phosphate solution, which had a radioactivity of 0.3×10^6 and contained $1\ \mu g\ ml^{-1}$ of PO_4-P as a carrier, were added to 2 l, of seawater in each aquarium in which 100-150 g of one of the reef components had previously been placed. An additional aquarium with no labelled phosphate added was used as a control. After an exposure of 3–5 h with periodic mixing of the water column each 15 min, subsamples from the aquaria were tested for the radioactivity of PO_4-P (r_t, in cpm ml^{-1}) and the absolute content of PO_4-P (P_t, in $\mu g\ P\ l^{-1}$). The value of r_t was estimated after precipitation of labelled phosphate with ferrous hydroxide in the presence of $CaCO_3$ as follows. To 25 ml of each subsample were added 1 ml of PO_4-P solution containing 1 μg of PO_4-P (as a carrier) and 1 ml of a mixture containing 2 g of NaOH + $CaCO_3$ + 3 g of ferrous ammonium sulfate in 100 ml of water; the mixture was shaken before use. The precipitates were collected on papers filters in a funnel 2 cm in diameter. Dried filters were placed in vials for liquid-scintillation count-

ing of their radioactivity (r_t). Estimations were made in triplicate: replicate filter counts varied within $\pm$ 5–7%. The PO_4-P contents (inorganic reactive phosphorus) were measured by the method of Murphy and Riley (1962). Values of radioactivity (r_i) and phosphorus content (P_i) also were estimated at the start of the exposure. Experiments with killed samples showed that the chemical uptake of $^{32}PO_4$ by them was negligible.

The rate of uptake (A_c) was calculated by the expression $A_c = [(r_i - r_t)\cdot(P_i + P_t)V]/[Wt(r_i + r_t)]$ μg P kg^{-1} h^{-1}, where t is the time (in h) of exposure. W is the dry weight (in kg) of substrate (coral colony, rubble, sand), and V is the volume of water (in l) in the aquarium. The rates of release of phosphate (A_e) were calculated on the assumption that the PO_4-P content of the water in each aquarium changes as a result of its metabolism by organisms associated with the substrate. Thus, the rate of change (A_t) is a balance value between the opposite flows of PO_4-P consumption (A_c) and its release (A_e), where $A_t = A_e - A_c$. Thus,

$$A_e = A_t + A_c, \text{ if } A_t = A_t = \frac{(P_i - P_t)\cdot V}{t\cdot W} \ (\mu g\ P\ kg^{-1}\ h^{-1}).$$

In those experiments in which the rates of phosphorus exchange (A_c, A_e, A_t) between soft-bottom biotopes (coral sands) and the water column were estimated, an enclosure technique was employed. Bottomless transparent and black plexiglass boxes measuring 30 x 30 x 30 cm were used as enclosures, each being fitted with a propeller to mix the water and a tube through which to add the isotope solution and take subsamples. These boxes were firmly seated on the coral sands, and aliquots of labelled phosphate solution were injected with a syringe. After the water inside the box had been thoroughly mixed by the propeller, subsamples of water were taken. After an exposure time of 3–5 h, a final set of subsamples was taken. In the subsamples, the initial and final radioactivities of PO_4-P (r_i and r_t, in cpm l^{-1}) and the initial and final PO_4-P contents (P_i and P_t, in g l^{-1}) were measured. To estimate a possible exchange of water between the enclosures and the surrounding water, thiosulphate solution was added to one of the boxes instead of labelled phosphate, and its concentration in the box was measured by iodometric titration at the beginning (k_i) and end (k_t) of the exposure of all boxes. A correction coefficient (K) was then calculated for the possible washout of PO_4-P from the boxes during the experiments: $K = k_t/k_i$. Its values varied from 0,85 to 0.95. Special experiments also showed that the chemical uptake and absorption of labelled PO_4-P from the water column during the time of the experiments (3–5 h) was negligible. The rate of uptake flow of PO_4-P from the water column into the coral sands (A_c) was calculated by the expression

$$A_c = \frac{V \times (r_i - r_t) \times (P_i + P_t)}{K \times t \times 0.09 \times (r_i + r_t)}\ \mu g\ P\ m^{-2}\ h^{-1},$$

where 0.09 is the bottom area (in m^{-2}) of the box, V is the volume (in l) of enclosed water, and t is the duration (in h), of the experiment. A_c values per day (24 h) were calculated from the A_c values per hour obtained in dark and transparent boxes. The rates of the opposite flows of PO_4-P, as well as the rate change in the PO_4-P content of the water resulting from its exchange with the bottom biotopes, were calculated in the same way as the corresponding values obtained in the aquarium experiments.

Results

Typical results of estimations of phosphorus exchange between living corals and surrounding water are shown in Table 1 and Fig. 1. They demonstrate that scleractinian corals, as well as soft octocorals possessing algal symbionts, both consume inorganic phosphate from the water and simultaneously excrete it. Usually, the flow of phosphate from water to coral (A_c) exceeded the opposite release flow (A_e), but at low ambient PO_4-P concentrations in the water (0.06–0.2 μmol l^{-1}), which are more typical of the reef waters of Heron Island than higher concentra-

Table 1. Flows of phosphate between living corals and water A_c – consumption; A_e – release; A_t – net shift of concentration of PO_4-P; P_i-PO_4-P concentration in control aquarium; temperature of water, 22 °C.

Coral	P_i (μmol·l^{-1})	Flows (μg P kg^{-1} h^{-1})		
		A_c	A_e	A_t
Pocillopora damicornis	0.3	75.1	46.5	− 28.6
	0.06	3.6	6.4	+ 2.8
Stylophora pistillata	0.3	28.9	13.9	− 14.5
Porites andrewsi	0.16	29.5	44.2	+ 14.7
Acropora squamosa	0.16	12.6	11.4	− 1.2
Cladiella sp. (hermatypic soft coral)	0.16	92.8	97.5	+ 4.7
Pacifigorgia sp. (ahermatypic soft coral)	0.26	78.6	2019.6	+ 1941.0
Leptogorgia sp. (ahermatypic soft coral)	0.26	34.7	2166.6	+ 2132.1

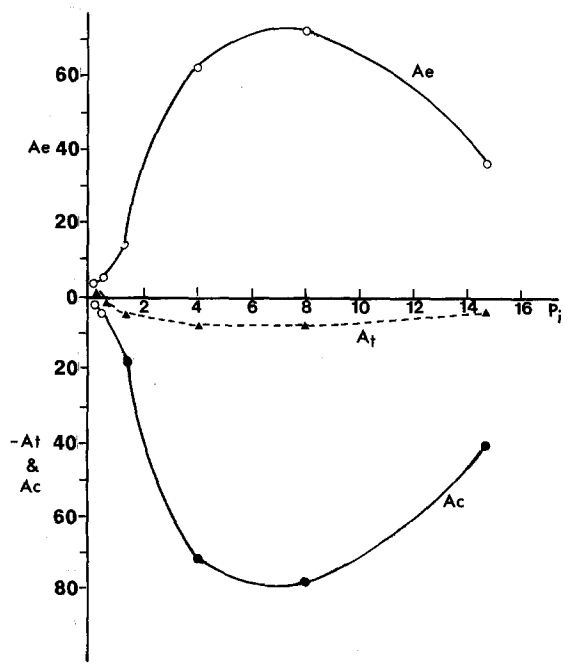

Fig. 1. Relationship between rates of uptake (A_c), release (A_e), and net uptake or release (A_t) of PO_4-P (μg P kg^{-1} h^{-1}) by a living coral, *Pocillopora damicornis*, and its concentration in the water (P_i, μmol l^{-1}).

tions, the release flow exceeded consumption. In such situations, a net increase of phosphate in the water occurred (A_t was positive). At higher ambient concentrations of PO_4-P in the water, the A_t values were negative, reflecting a net uptake of phosphate by coral from the water, but it was 2–10 times less than the absolute rate of uptake (A_c), being masked by the simultaneous release of PO_4-P from the coral colony ($A_t = A_c - A_e$). In the ahermatypic gorgonians investigated (Table 1), the uptake flow (A_c) was negligible compared with the release flow (A_e), comprising only 2.3% of the latter. Thus, ahermatypic soft corals are unable to compensate for inorganic phosphate loss via simultaneous consumption of PO_4-P from the surrounding water, as hermatypic corals do. Their phosphorus intake requirements are achieved by heterotrophic feeding.

Rates of PO_4-P consumption (A_c) in the dark were usually somewhat less than in the light, but the dark release rates (A_e) increased some 10–15%. Net uptake (A_t) thus approached zero in the dark, though the fluxes of PO_4-P remained high, being commeasurable with those on light (Fig. 3).

In Table 2 and Figs 2 and 3 results are presented for aquarium experiments measuring the phosphate exchange between the water and communities within corals sands and in the periphytonic overgrowth that covers coral rubble, dead coral and flat rock. These estimations show the existence of the same two opposite flows of PO_4-P uptake (A_c) and release (A_e), same as in living corals, reflecting the presence of autotrophic producers and heterotrophic decomposers in the periphytonic communities and on the grains of coral sand (Sorokin, 1981). The autotrophic and heterotrophic components in these habitats are functioning in a narrow interconnection, being united

Table 2. Phosphate flow rates between components of bottom biotopes and water during daytime on light; designations – see Table 1.

Component	P_i $\mu mol\ l^{-1}$	Flows of phosphate				
		($\mu g\ P\ kg^{-1}\ h^{-1}$)			($mg\ P\ m^{-2}\ day^{-1}$)	
		A_c	A_e	A_t	A_c	A_t
Flat rock covered with periphyton	0.35	18.2	15.1	− 3.1	2.2	− 0.4
Coral rubble from reef flat	0.35	31.0	18.0	− 13.0	3.7	− 1.6
	0.16	11.5	21.5	+ 10.0	1.4	+ 1.2
Piece of dead branch colony of coral Stylophora, covered with periphyton	0.35	56.0	53.9	− 2.1	12.1	− 0.5
	0.16	14.6	17.4	− 2.8	3.2	+ 0.6
Living branch of same colony	0.35	51.7	28.8	− 22.9	11.2	− 4.9
	0.16	12.6	11.4	− 1.2	2.3	− 0.2
Coral sand from reef flat	0.35	15.2	23.2	+ 8.0	2.9	+ 1.5
	0.16	6.1	11.2	+ 5.1	1.2	+ 0.9

within mucous structures (Johannes *et al.*, 1972) somewhat as in living corals. This metabolic interconnection facilitates the internal recycling of nutrients and decreases their release to surrounding waters.

The similarity of metabolic patterns in periphyton and living corals is also reflected in the coincidence of the absolute values of phosphate uptake and release flows calculated per unit dry weight of substrate. This coincidence was most striking when the experiments involved the same coral colony, a part of which was living and a part of which was dead and covered with periphyton (Table 2). Photosynthesis and respiration rates also appear to be commeasurable in living and in dead parts of coral colonies. Their ratio in them varied in our experiments: of photosynthes rates – within 0.7 to 1.6 (average 1.2) and of respiration – within 0.5 to 2.1 (average 1.4) – see Table 3. The rates of phosphate flows (A_c and A_e) in periphyton appear to be the larger but are dependent on the concentration of PO_4-P in the water as well as on their balance (A_t). At low

Table 3. Rates of photosynthesis (P) and respiration (R) in two part of the same coral colony (living, and dead and covered with periphyton) and in coral rubble. Values of P and R measured in light and dark enclosures and expressed as $\mu g\ C\ day^{-1}\ g^{-1}$ dry weight of coral.

Component	Part of colony	P	R	P/R
Coral	Living	227	196	1.4
Pocillopora damicornis	Dead	312	247	1.3
Coral	Living	296	207	1.5
Acropora sp.	Dead	182	98	1.8
Coral *rubble*	–	273	110	2.5

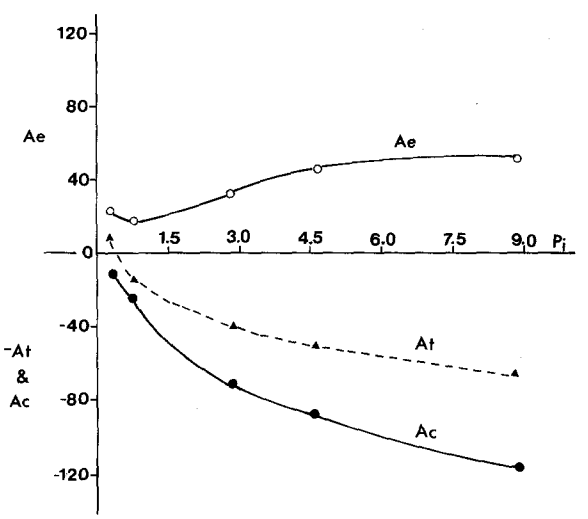

Fig. 2. Relationship between rates of uptake (A_c), release (A_e), and net uptake or release (A_t) of PO_4-P by coral rubble covered with periphyton, and concentration in the water column (P_i, $\mu mol\ l^{-1}$).

ambient PO_4-P concentrations (0.1–0.3 μmol l^{-1} are usual for Heron Island reef waters), the rates of PO_4-P consumption (A_c) by periphytonic overgrowth on different kinds of substrate varied within 10–60 μg P kg^{-1} h^{-1}; i.e. it was comparable with A_c in living corals (Tables 1 and 2). In most of the experiments with periphyton, the A_c and A_e flows were comparable, but the excretion flow (A_e) was less dependent on ambient PO_4-P concentration.

An increase in phosphate concentration from 0.1 to 2–3 μmol l^{-1} caused an increase in the rate of its consumption by periphyton (Fig. 2) and a weak increase in the release rate (A_e). At PO_4-P concentrations between 3 and 9 μmol l^{-1}, the consumption rate stabilized, comprising 30–70% of the consumption rate at this high PO_4-P concentration. The net uptake (A_t) at a high concentration of PO_4-P in the water was 20–70% of the absolute rate of PO_4-P uptake (A_c). Light conditions influenced the rate of phosphorus flow between water and periphyton, and this was also observed in experiments with coral sand (Fig. 3, Table 4). As with living coral, some decrease in the uptake rate (A_c) occurred in the dark, with a simultaneous increase in the release rate (A_e). In the dark, the balance therefore shifted to the side of release, and thus net uptake (A_t) decreased. Sometimes in the dark, A_t values were positive; instead of a net uptake, a net release occurred. This situation was observed in the coral-sand aquarium experiments (Fig. 3) as well as *in situ* (Table 4). These observations correspond with data in the literature demonstrating that, in *in situ* experiments with coral sand, a very low rate of net change in ambient PO_4-P concentrations usually occurs (Propp *et al.*, 1983).

Calculations of the flow of phosphate between bottom biotopes covered by coral rubble and the water column gave values of 3–10 mg P m^{-2} day^{-1} (Table 2). Similar estimations for coral sand, determined in *in situ* enclosures, resulted in values of 2–7 mg P m^{-2} day^{-1} (Table 4). At the same time, the net uptake (A_t) of PO_4-P was very low. This reflects one of the most important features of nutrient metabolism in coral reef ecosystems – its semiclosed character in bottom biotopes, which limits the losses of inorganic

Table 4. Flow rates in phosphate exchange between soft botom reef biotopes and the water column as measured in enclosures *in situ* designation – see Table 1; light and dark – experiments in transparent and black boxes, respectively.

Place; characteristics of bottom; depth at low tide	P_i μmol l^{-1}	Time of experiment	Illimination conditions	Flows of PO_4-P (μg P m^{-2} h^{-1})			(mg P m^{-2} day^{-1})	
				A_c	A_e	A_t	A_c	A_t
Flat opposite N.E. coast of island; coral sand covered with layer of diatoms; 0.5 m	0.28	11 a.m.	Light	326.6	190.8	−135.8	7.68	−1.77
			Dark	313.3	302.9	−10.4	–	–
Flat of N.W. coast of island, opposite resort coral sand; 0.7 m	0.22	12 noon	Light	195.2	168.8	−26.4	3.58	+0.68
		5 p.m.	Dark	403.5	186.0	+82.5	–	–
Bottom area in Shark Bay (S.E. end of island); 0.8 m	0.16	12 noon	Light	135.8	145.4	−20.4	4.7	+0.92
		4 p.m.	Dark	117.9	197.3	+105.9	–	–
Shallow northern part of lagoon; fine sand; 3 m	0.06	11 a.m.	Light	67.6	48.8	−18.8	1.63	+0.08
		4 p.m.	Dark	68.7	98.8	+25.1	–	–
Central part of lagoon near patch-reef; 6 m	0.17	11 a.m.	Light	161.0	87.0	−74.7	3.73	−1.07
		2.3 p.m.	Dark	144.9	135.0	−9.3	–	–
Outer leeward reef in N.E. part of atoll; midgrained coral sand between two ridges; 8 m	0.19	12 noon	Light	248.0	147.0	+50.7	4.7	+0.92
		3 p.m.	Dark	144.2	270.8	+126.7	–	–

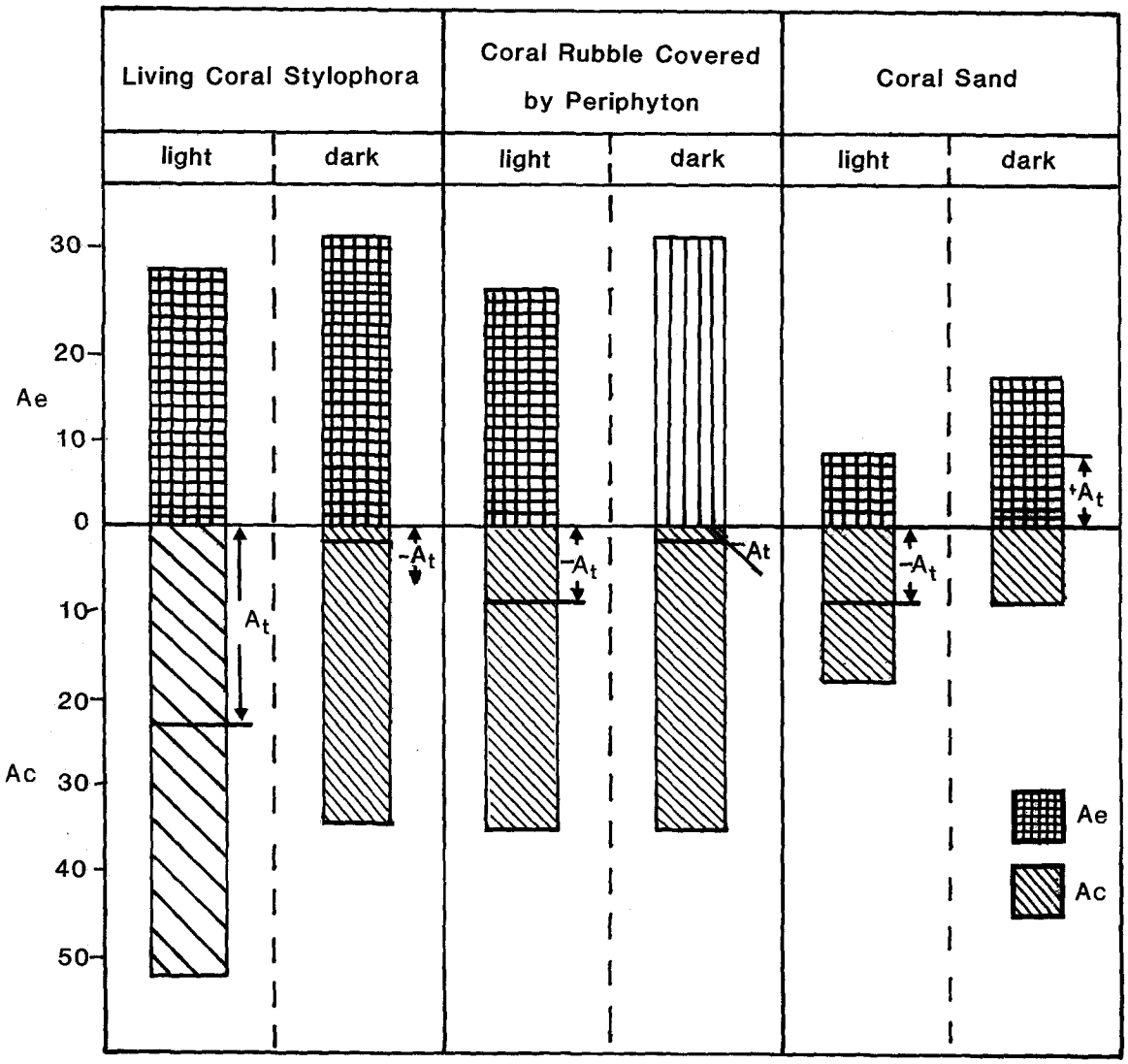

Fig. 3. Rates of PO_4-P flow (A_c, A_e, and A_t; see text) in elements of reef bottom biotopes as influenced by light conditions.

nutrients from the bottom to the water column because of its internal recycling within the structures of the periphytonic communities (Johannes *et al.*, 1972) and within the tissues of symbiotic benthic animals (Pomeroy *et al.*, 1974). In fact, in bottom biotopes occupied by living coral or coral rubble, and with a low ambient PO_4-P concentration in the overlying water (0.1–0.3 μmol l^{-1}), the values of net uptake or release (A_t) approach zero. In coral sand the *in situ* enclosure experiments showed (Table 4) that A_t values were often slightly positive because a net release of PO_4-P occurred within the 24-h balance, its rate varying from 1 to 3 mg P m^{-2} day^{-1}.

Discussion

The existence of two-way flows of phosphate between living coral and the surrounding water, and the predominance of its release over consumption at low ambient concentrations in the water, demonstrate that some former estimations of PO_4-P uptake by coral, made by simply measuring the net change of its concentration in the water in the

presence of a coral colony, underestimates the actual rates of exchange. This should influence the kinetic curves of uptake since they are dependent on PO_4-P concentrations in water (reviewed by Muscatine, 1980). For example, in accordance with the kinetic data, the lower limit of concentration at which the consumption of PO_4-P by coral starts is about 0.2–0.3 μmol l^{-1}, but a concentration of 0.1–0.2 μmol l^{-1} is typical in most reef waters. The data obtained by measuring uptake flow (A_c) with the aid of labelled phosphate are high even at low ambient levels of PO_4-P in the water, but it is masked by simultaneous release (A_e). It is therefore impossible to determine uptake by measuring only the net change in phosphate content (A_t).

In addition to excreting inorganic nutrients, corals also excrete their organic forms (Johannes & Webb, 1970; Muscatine & D'Elia, 1978). A significant part of the release of organic nutrients proceeds via the secretion of mucus. With respect to their total phosphorus balance, corals, even the hermatypic ones, release more soluble organic and inorganic phosphorus than they consume (D'Elia, 1977). Nevertheless, their ability to consume ionic phosphate from the surrounding water in much the same way as plants diminishes the net release in comparison with ahermatypic corals and other non-symbiotic animals (Lewis, 1973; Muscatine & Porter, 1977; Propp, 1981; see Table 1). The main source of phosphorus uptake in hermatypic corals is surely their heterotrophic feeding on zooplankton and other particulate organic matter (Johannes *et al.*, 1970).

As noted above, the ambient PO_4-P concentration remains rather stable in water passing over an actively functioning reef. Changes in it are small and have a non-predictable direction even at very low ambient concentrations, the stock of PO_4-P seeming to be consumed by reef bottom autotrophes within a few hours or even several tens of minutes (Atkinson, 1983). But this does not actually happen (Pilson & Betzer, 1973). As can be deduced from the above data, the striking stability results from a sequence of balanced flows of PO_4-P between the water column and bottom biotopes of the reef in the autotrophe-heterotrophe system. One of the important causes of the equilibrium of PO_4-P within benthic communities of the reef should be a reciprocal equilibrium in carbon flows (Table 3). In benthic communities, the ratio between photosynthesis and respiration usually approaches one (0.7–1.3, Lewin, 1977). Equalization of the nutrient flow between the water column and reef bottom biotopes probably also explains the stabilization of their concentrations at a low level in waters over reefs, even in conditions of extensive external input by pollution (Johannes, 1973; Kimmerer & Walsh, 1981) or artificial fertilization (Kinsey & Domm, 1974). This can be so even when such inputs cause obvious changes in the community structure of the bottom biotope, or even if they cause changes in the ratio of photosynthesis to respiration (Wiebe, 1985).

In discussing the exchange rates of phosphate between the bottom and the water column in coral reefs, it is also necessary to take into account the fact that reef bottom communities usually contain, simultaneously, coral rubble covered with periphyton, living corals, and benthic fauna. Thus, the bottom communities can consume not only inorganic phosphate but also organic phosphorus in dissolved form or in compounds of suspended food material (detritus and plankton) that are consumed by periphytonic microflora and benthic animals. This flow of organic phosphorus from the water column into the bottom biotopes was not accounted for in the present study, but (together with the consumption of inorganic phosphate) it surely provides the positive balance of phosphorus in the coral reef ecosystem during its interaction with oceanic waters, in spite of some net release (A_t) of inorganic phosphate into the water column by the bottom biotopes. Such an additional input of organic phosphorus into the bottom biotope could play a very important part in its build-up in bottom sediments, and in rock material of coral reefs (Entsch *et al.*, 1983), so it needs careful evaluation.

These observations also support the view that the main mobilized stock of nutrients in the coral reef ecosystem exists in the living biomass of organisms and, to a lesser extent, in the detritus

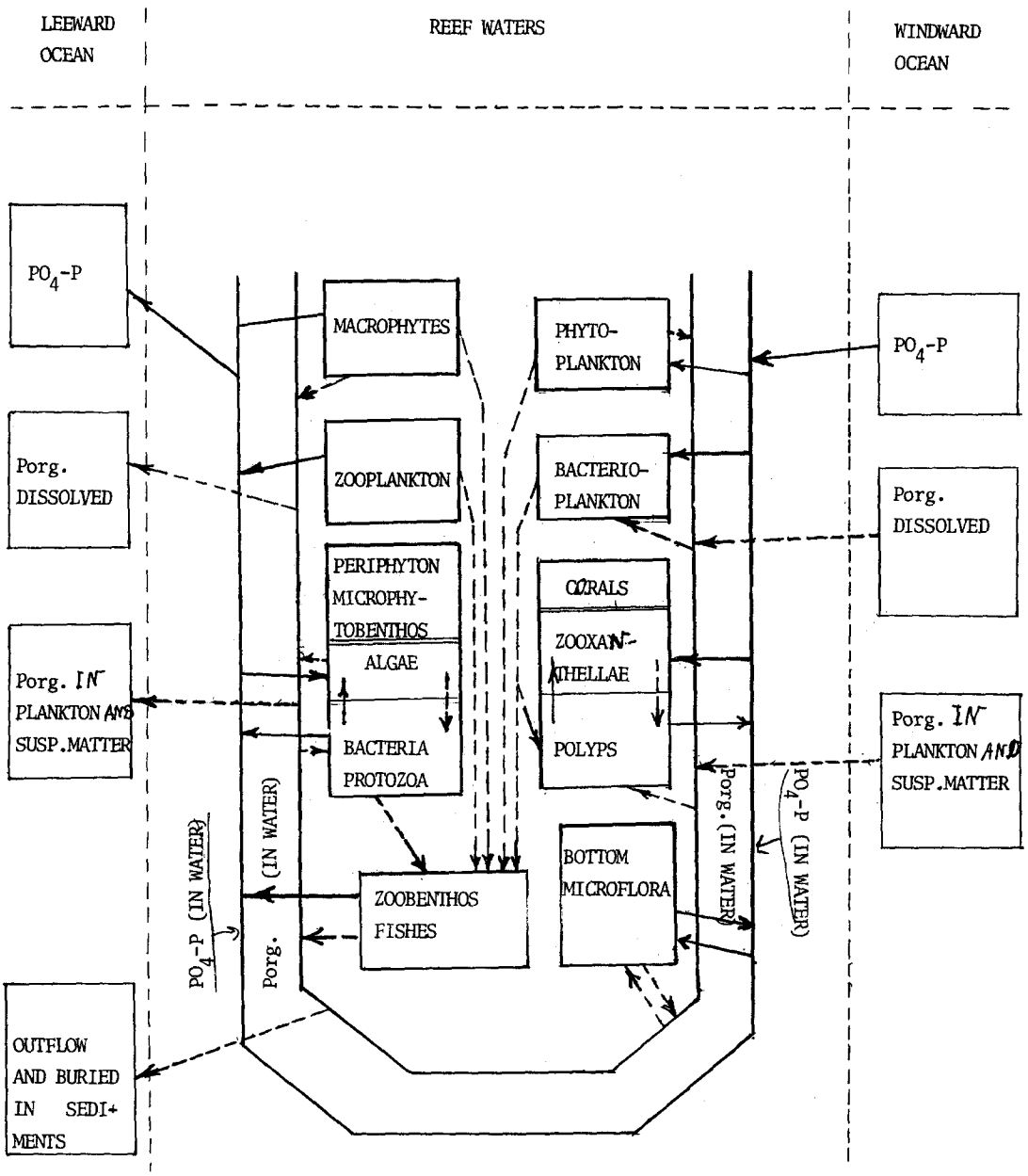

Fig. 4. Scheme of phosphorus metabolism in coral reef ecosystem.

(Hatcher, 1985). Direct estimations of this stock are lacking, but its approximate computation appears to be possible on the basis of the total stock of organic matter in the bottom reef biotopes, which Lee *et al.* (1975) estimated at about 50–130 g C m^{-2}. It average ratios of C : N = 10–12 and C:P = 50–70 (by weight) are accepted, then the possible stock of nitrogen in reef biotopes will be about 5–15 g m^{-2} and that of phosphorus about 0.7–2.5 g m^{-2}. If the flow rates of phosphorus between the bottom and the water column, in accordance with the above data (Tables 2 and 4) are within 3–10 mg P m^{-2} day^{-1}, then the corresponding flow rates of nitrogen (by stoichiometry) should be within 40–150 mg m^{-2}. Thus, the turnover rates of P and N should be about

2–4 months, which appears to be fast enough, realizing that a significant part of this stock of nutrients exists in the biomass of large organisms: fishes, macrobenthos, macrophytes. A provisional scheme of phosphorus metabolism in reef ecosystem is given in Fig. 4.

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