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PHOSPHATE METABOLISM OF CORAL REEF FLATS

University of Hawaii PH.D. 1981

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PHOSPHATE METABOLISM OF CORAL REEF FLATS

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

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ABSTRACT

The present dogma on coral reef metabolism suggests that there is little exchange of phosphate between the benthic community and the water overlying that community. The reef's nutritional requirements supposedly are met by cycling or retention within the benthic community. I posed the hypothesis that the phosphate needs of the reef producers could be met through exchange with the water column, and that net changes of phosphate in water as it flows over reef communities reflect net metabolic processes.

Phosphate uptake experiments were conducted on collections of reef organisms incubated in aquaria. Extensive field sampling was performed to determine the net changes of phosphate over the Kaneohe Bay barrier reef flat. Carbon, nitrogen, and phosphorus ratios were determined for reef autotrophs.

Results of these experiments indicate that the uptake rate of phosphate is proportional to the reactive phosphate concentrations, and that at ambient phosphate concentrations of 0.15 uM the uptake and release of phosphate between the reef benthos and the water column is approximately 0.1% of community dark respiration (mole P uptake/mole O_2 respired). The field results demonstrate that the depletion of phosphate over the reef flat may be used to measure net community carbon production if the C:P ratio of the reef autotrophic organisms (approximately 500-650) is used to scale phosphorus uptake to net carbon production. It is reasoned that recycling of phosphorus for a whole reef flat is not tight, and the system can depend primarily on exchange with the water column for its nutrients. The high advective flux of phosphate over most reef flats

encourages a large biomass system, whereas the low concentration of phosphate probably influences the growth rate per biomass of most reef primary producers.

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I. INTRODUCTION

A. Primary Production

There are two ways of expressing primary productivity: gross primary production and net primary production. Gross primary production is the total carbon (C) assimilated by primary producers over a 24-hour period, and it is directly related to the photosynthetic ability of the system. Net primary production is the difference between the total carbon assimilated and the total carbon respired by the primary producers over a 24-hour period. Net community production, on the other hand, is the net carbon production of the whole community: producers and consumers. This net carbon production is related to the ability of the system to create new biomass (Odum, 1971).

Gross primary production (P) and respiration (R) of coral reefs are high. The net production, as measured by the difference between photosynthesis and respiration over a 24-hour period (P-R) (see Kinsey, 1979), is variable, and often low. Kinsey (1979) has introduced the principle of the "standard reef," in which the gross photosynthesis to respiration ratio (P/R) is 1. Community photosynthesis and respiration can be determined by measuring changes in oxygen (O_2) or carbon dioxide (CO_2) in water over coral reef flats.

The standard reef has a net community production near 0 (P-R=0). If gross primary production is greater than respiration over a 24-hour period, P-R is greater than 0 and P/R is greater than 1. Likewise if community respiration is greater than primary production, P-R is negative and P/R is less than 1. Coral reef flats as whole ecosystems have P/R ratios between 0.8 and 1.2 (Kinsey, 1979). A P/R ratio greater than 1 means that the reef can produce enough reduced carbon to support itself,

while a P/R ratio less than 1 suggests that the reef needs an external source of metabolizable carbon. Coral reef flats also are zoned metabolically. Fore-reef environments, those closest to incoming ocean water, are net carbon producers while communities in the back areas of reef flats are net consumers (see Kinsey for details of reef zonation). Even though there is metabolic zonation, the reef flat as a whole usually has no net carbon production, or a P/R = 1. Carbon is believed to be transfered as particulate material from the fore-reef to the back-reef where it is consumed. Different transects on a coral reef flat however have different net community productivities. At Enewetak Atoll the net community productivity of an algal dominated reef flat was high (approximately 500 mmoles C m^{-2} day^{-1}) while that of a coral dominated reef flat was not significantly different than 0.

Odum (1971) states that the disappearance of raw materials such as nitrogen (N) and phosphorus (P) can be used to measure the net carbon production of the whole community. The net community productivity is calculated by equating the net uptake of N or P to C by the following equation (Odum, 1971):

1,300,000 Cal. radiant energy + 106 CO_2 + 90 H_2O + 16 NO_3 + 1 PO_4 + mineral elements = 13,000 Cal. potential energy and 3258 gms protoplasm (106 C, 180 H, 46 O, 16 N, 1 P, 815 gms mineral ash) + 154 O_2 + 1,287,00 Cal. heat energy dispersed (99%).

The above equation uses the familiar Redfield ratio (Redfield et. al., 1963). This relationship between C:N:P (106:16:1 by moles) has been widely used to explain distributions of nutrients (N and P) in the

ocean (Redfield et. al., 1963) and also to estimate the net community production (i.e. creation of new biomass) in oceanic regions (Steele, 1958; Steeman-Nielson, 1963; and Redfield et. al., 1963). The surface waters of the ocean generally contain low concentrations of inorganic N and P relative to the deep water. These nutrients have been removed from the water by phytoplankton and have been made into plankton biomass of C:N:P composition 106:16:1. The nutrients N and P are therefore incorporated into the foodweb in the surface ocean and recycled until they are removed as falling particles (living or dead). The particulate material is then fully decomposed in deeper ocean water to the inorganic forms of N and P. Vertical advection and vertical turbulance bring nutrients to the surface, stimulating primary production. The Redfield ratio has been extensively used to compare recycling and regeneration processes involving C, N, and P in the ocean.

The use of net changes in nutrients to measure net community production of coral reef ecosystems has been extremely limited. In only one study were nutrients (P in this case) used to estimate net community production of a coral reef environment (Smith and Jokiel, 1977). Net community production of coral reef flats is usually estimated by calculating the difference between photosynthesis and respiration (Sargent and Austin, 1949; Odum and Odum, 1955; Smith and Marsh, 1973; and more recently, Kinsey, 1979).

This dissertation demonstrates that net community production of coral reef flats can be measured using the net uptake of phosphate by the system. I posed the hypothesis that phosphate in the water overlying the reef exchanges readily with the benthic community and that the phosphate needs of the reef producers can be met through this exchange. Changes in

phosphate concentration of water as the water flows across reef flats therefore reflect net gains or losses of biomass.

The present dogma of coral reef metabolism, however, suggests that there is little exchange of phosphate between the reef producers and the water column. The nutritional needs of these producers are believed to be met through cycling within the benthic community.

B. Nutrient recycling

Odum (1971) makes the following distinction between tropical and temperate ecosystems: "Nutrient cycling in particular and community control in general, then, tend to be more 'physical' in the north and more 'biological' in the south." I interpret this broad statement to mean that nutrient recycling in higher latitude ecosystems tends to be controlled by abiotic factors and nutrient recycling in lower latitude ecosystems tends to be controlled by biotic factors. As an example of a tropical ecosystem that has "solved the nutrient cycling problem," Odum discusses the coral reef as a highly evolved system that has intricate recycling mechanisms between autotrophs and heterotrophs. The coral-algal symbiosis is the example he described (Odum, 1971). It is generally believed that there is little exchange of nutrients between the reef benthos and the overlying water column. Instead, nutrients are held or retained within the reef structure, enabling photosynthesis to occur at a rapid rate. Undoubtedly nutrient retention occurs; however, stressing symbiosis as a nutrient recycling mechanism implies that reefs could not have a high primary productivity without symbiotic relationships. It is also implied by Odum that "symbiosis" is much different than nutrient

retention by any other producer. Other mechanisms of nutrient recycling within the benthos have not been described.

The atoll coral reef is typically described as being an "oasis in a desert;" the desert being the low nutrient, low productivity tropical ocean. (Tropical waters tend to have lower nutrient concentrations and lower primary productivity than coastal temperate waters). Nutrients are retained and effectively recycled within the reef ecosystem, thereby creating a kind of an oasis. Symbiosis has always been implicated as the mechanism responsible for nutrient recycling in coral reef ecosystems.

Recently however, atoll reef flats have been described as exporting large amounts of nitrogen (Webb et. al., 1974). Nitrogen fixing organisms (showing nitrogenase activity, not necessarily the conversion of ^{15}N to organic compounds) appear to be abundant on reefs (Capone et. al., 1977). Nitrogen therefore might be "loosely" recycled in the system: the reef community retains sufficient nitrogen to maintain itself, and exports the excess (Johannes et. al., 1972). The nitrogen fixation capacity of a reef flat is large, approximately equivalent to an alfalfa field on an area basis.

Phosphorus, on the other hand, has been said to be "tightly" recycled (Johannes et. al., 1972). This conclusion probably originated from observations that the concentration of phosphate does not change as water flows over atoll reef flats. Early investigators (Sargent and Austin, 1949; Odum and Odum, 1955) measured phosphate concentrations in water upstream of a reef flat and downstream of the same reef flats. Even though concentration changes were noted, these early workers believed they were not analytically different. The gross productivity of the coral reef flat was large and the P/R ratio was near 1 (Odum and Odum, 1955).

Pilson and Betzer (1973) however measured statistically signficant differences in phosphate concentrations in the water as it crossed a reef flat transect dominated by algae, but found no difference over a transect dominated by corals. Pilson and Betzer did not use these differences to measure net productivity of the system. Instead, they showed that hourly changes in phosphate concentrations were not correlated with hourly changes in oxygen concentrations scaled to phosphate by the Redfield ratio. The Redfield ratio is not applicable to an instantaneous gross productivity measurement. Since the fluxes of oxygen are correlated with light in the normal diurnal relationship, the oxygen fluxes are "instantaneous," not net values, even though all the carbon produced may be new cellular material. The uptake and release of phosphate does not follow the instantaneous uptake and release of oxygen. Net community processes are better discussed daily, weekly, and seasonally (Odum, 1971).

Smith and Jokiel (1976) recognized that the loss of phosphate from the water had to equal net productivity and used the decrease of reactive phosphate in Canton Atoll Lagoon to estimate net productivity of the entire lagoon. Whereas Pilson and Betzer (1973) used the Redfield ratio to match carbon to phosphorus on an hourly basis, Smith and Jokiel (1976) used the Redfield ratio to match carbon to phosphorus on the time scale of a month. The net community production of Canton Atoll Lagoon was determined to be 1% of the gross productivity using this method.

The scant research on phosphate of reef ecosystems has convinced many investigators that there is little to be learned from the phosphate flux between the reef and the water column. The idea of tight phosphate recycling within the reef structure is generally accepted. Does phosphate remain constant over some reef flats because it does not interact

with the benthos, or does it exchange readily, therefore reflecting the net productivity of the system? Ihis is the major question of this dissertation. The water column might be a primary source and sink of phosphate for the reef organisms.

C. Study reefs

Chave (Smith et. al., 1973) has defined a coral reef as, "...a magnificent and complex community of marine organisms which are able collectively, through the formation of limy ($CaCO_3$) skeletons, to construct, modify, or maintain a shore environment." Ihis definition encompasses a variety of reef structures and reef communities.

Ihere are generally three kinds of coral reefs: fringing reefs, barrier reefs, and atolls. Fringing reefs extend outward from land and grow seaward; barrier reefs are separated from land by a lagoon; and atolls are open-ocean reefs growing on the tops of submerged volcanic islands. All of these reefs maintain organisms which are both constructive and destructive to the inorganic ($CaCO_3$) reef structure.

Coral reefs have diverse assemblages of organic carbon producers and consumers. Producers on a reef include: thalloid macroalgae, seagrasses, algal mats, filamentous algae in living corals and dead substratum, encrusting calcifying algae, nitrogen-fixing blue-green algae, symbiotic unicellular algae, and a whole suite of benthic unicellular algae. Herbivores and consumers include: corals, fish, anemones, sponges, annelid worms, large and small crustacea, echinoderms, mollusks, nematodes, and protozoan . Reefs generally have an abundant biomass of producers with a smaller herbivore and consumer biomass (Odum, 1971).

The reefs at Enewetak Atoll, Marshall Islands are about 300-500 meters wide. Open ocean waves break on the "fore-reef;" water from these waves moves over the reef flat into the lagoon. The reef flats are shallow, being only 1 - 2 meters deep, and usually parts are exposed to the air at low tide. The oceanic water flows across these barrier reef flats as water flows over a stream bed. The residence time of water on such a reef flat is only 10-30 minutes.

Enewetak reef flats can be zoned according to the composition of organisms and community metabolism. The fore-reef and algal ridge (where waves break) have many encrusting, sturdy producers. The P/R ratio of this community is greater than 1. The reef flat behind the algal ridge is also a net producer, but shows an increase in filamentous and turfy algae. The back regions of the reef, or "back-reef", have P/R ratios less than 1, and usually have well developed coral communities. The net production of organic material in the fore-reef environment is consumed in the back regions of the reef flat. The reef as a whole produces calcium carbonate sands which are swept into the lagoon by wave action.

The Kaneohe Bay barrier reef, where much of this research was conducted, is somewhat similar to the Enewetak reef flats. The important difference for this work however is that water resides much longer over the Kaneohe barrier reef flat than over the Enewetak reef flats. The Kaneohe Bay reef flat slopes into the ocean gradually, hence ocean water is not driven over the reef. Since the advective flow of water is slower and the reef flat about five times wider in Kaneohe Bay than at Enewetak the water over the Kaneohe Bay reef has a long residence time, near 10 hours. This is sufficient to measure an increase in salinity over the reef (Appendix A). The Kaneohe Bay reef also shows metabolic zonation,

however the zones are not as distinct as the Enewetak reef flats (Appendix A). The reef flat can be divided into three general zones: a fore-reef algal zone; a coral-algal zone, and a seagrass zone. The fore-reef algal zone produces organic material (Webb, 1977) and the seagrass zone consumes this material (Appendix A). The horizontal profiles of these reef flats are shown in Figure 1.

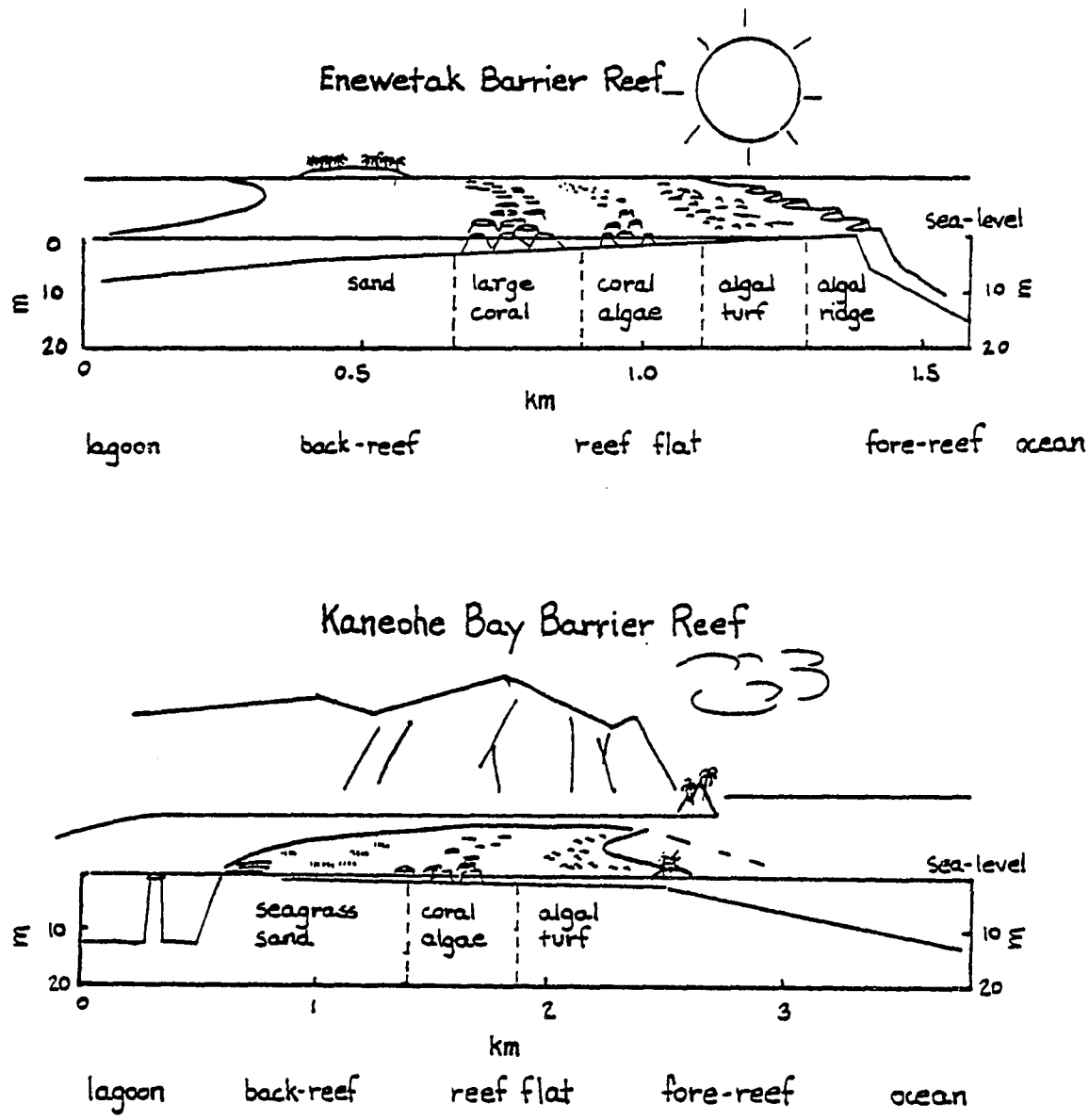

Figure 1: Horizontal profiles of Enewetak and Kaneohe Bay barrier reefs. Note the difference in width of the two reefs.

II. REVIEW OF RESULTS

Experiments were designed to answer the following questions: (1) To what extent does phosphate exchange with the reef benthos at ambient phosphate concentrations? and (2) Can phosphate depletion in water over a reef flat be used to measure net community production?

The exchange experiments were conducted on a mixed reef community in aquaria by adding phosphate to aquarium water and following the uptake of this nutrient. A typical time course for reactive phosphate (RP, also called dissolved inorganic phosphate, DIP) and total phosphate (IP) during such an experiment is shown in Figure 2, page 17. The initial concentrations were low and represent reef flat water. When the organisms were added to the aquaria, reactive phosphate concentrations increased, presumably from the loss or excretion of phosphate by the organisms. Uptake of phosphate was demonstrated when high concentrations of reactive phosphate were added to the incubation water, in this example with 2uM reactive phosphate. Community respiration rate was measured by the depletion of oxygen in the aquarium while in the dark. I am assuming that this measured respiration rate is a good estimate of community "metabolic biomass." No assumptions are made regarding the difference between light and dark respiration. All phosphate uptake rates were normalized to the respiration rate of the mixed reef community. At low ambient concentrations of phosphate, these communities released reactive phosphate and total phosphate. To determine whether uptake of phosphate occurred at low phosphate concentrations, two ^{32}P additions of extremely low concentration were conducted. Both of these experiments showed a rapid uptake of ^{32}P and a net increase of reactive phosphate and total phosphate (Figure 4, page 21). This uptake demonstrates qualitatively that phosphate was

exchanged rapidly with the benthos. The ^{32}P uptake rate, normalized to dark respiration, was determined by solving the differential equations of Caperon et. al. (1979). The uptake rates were plotted as a function of concentration (Figure 8, page 33). At low phosphate concentrations the uptake rate was approximately proportional to the concentration. At concentrations of reactive phosphate found over reef flat communities the uptake rate was approximately 0.1% of dark respiration (mole P uptake/mole O_2 respired).

Adsorption of phosphate was demonstrated to be minimal compared to phosphate uptake by the community. Also, to demonstrate that phosphate was incorporated into the cells, and not just adsorbed, ^{33}P (a lower energy isotope than ^{32}P) radioactivity was measured in nucleic acids of reef autotrophs after short incubations in ^{33}P orthophosphate. It was concluded from these experiments that phosphate exchanges rapidly with the benthos. The net changes observed in the field therefore can be a result of net interactions with the benthos.

Field data were collected to establish whether there was a net decrease in phosphate over reef flats and whether such a decrease can be related to net community production. Illustrations of the net uptake of phosphate over the Kaneohe Bay reef are shown in Figures 11-13, page 53-55. Reactive phosphate and total phosphate are shown to be significantly lower over the reef than in the adjacent ocean and bay. As water flows over the reef, the benthic system exchanges phosphate with the water column. The net decrease observed, Figures 13, page 55, was therefore related to the production of new biomass. The rate of uptake of phosphate from the water column was calculated. To scale the net uptake of phosphate to carbon, the mean C:P ratio of the producers was used rather

than the Redfield ratio (106:1). Algae and rubble samples were analyzed for their C:N:P ratios. The average C:P ratio for Kaneohe Bay producers was 640:1. This ratio, 640:1, was therefore used to convert phosphate depletion in the water to net community production in terms of carbon. The mean C:P ratio for Enewetak producers was 490:1. This ratio was also applied to phosphate depletion of water flowing over Enewetak reef flats (data collected by Pilson and Betzer, 1973). Net community production as calculated by phosphate depletion and scaling to carbon (C:P = 490:1) was compared to net primary production (as calculated by the daily difference between photosynthesis and respiration, using CO_2 and O_2 to measure gross primary production) in Table 6 (page 61). The results show that phosphate can be used to estimate net community production if a C:P ratio of the substrate organisms is used to scale phosphate depletion to carbon uptake.

It is concluded that phosphate is exchanged (uptake and release) rapidly with the reef benthos at a rate approximately 0.1% of dark respiration (mole P uptake/mole O_2 respired) and that phosphate depletion of water over a benthic system can be used to calculate net community production if a C:P ratio of approximately 500-650 is used to scale phosphorus to carbon.

III. EXPERIMENTS

The methods and results to each of the following five groups of experiments will be discussed separately:

A. Phosphate exchange experiments

B. Alkaline phosphatase assays

C. Adsorption experiments

D. Nutrient water sampling

E. Producer CNP ratios

The first 3 groups of experiments (A, B, C) were performed to determine whether phosphate exchanges with the reef flat benthic community, and if so, whether dissolved organic phosphate compounds and physical adsorption of phosphate to the substratum influences the exchange. The data sets were obtained by incubating collections of organisms in aquaria. The last two groups of experiments (D, E) were conducted in the field (Kaneohe Bay barrier reef) and used to determine whether phosphate is depleted over a reef flat, and if so, if this depletion could be used to measure net community productivity of the reef flat. The methods and results for each experiment are discussed below.

A. Phosphate Exchange Experiments

These exchange experiments were conducted to determine the uptake rate of phosphate as a function of phosphate concentration.

Methods:

Complex communities of benthic material were collected from the Kaneohe Bay barrier reef flat and immediately transported to the Hawaii Institute of Marine Biology (HIMB). The sample communities were heterogeneous; they included coral, rubble, coralline algae, and macroalgae.

These reef substrata were placed in an aquarium filled with freshly collected reef water and the incubation was begun. To measure the uptake rate of phosphate at higher than ambient phosphate concentrations, phosphate was added to the incubation water as a solution of orthophosphate (K_2HPO_4) mixed in about 100 ml of seawater. Once the phosphate was added, the aquarium water was mixed with a stirring rod or by rocking the aquarium. Water was mixed after each sampling period. To measure the uptake rate of phosphate at ambient phosphate concentrations orthophosphate was added to the incubation water as ^{32}P. Since the ^{32}P is carrier-free (nearly "pure" ^{32}P), the concentration of the added phosphate can be measured to very low levels by measuring the radioactivity of the water sample. At low (ambient) phosphate concentrations, if uptake and release of phosphate by the reef community occurs at the same rate, the chemically measured reactive phosphate will remain constant while the ^{32}P will decrease in the incubation water.

Samples of the aquarium incubation water were taken periodically to determine any changes in reactive phosphate, total phosphate, and ^{32}P throughout the incubation. Water samples were taken with a plastic 50 ml syringe and the water was immediately filtered through a 0.45 um. precombusted and rinsed GFC glass fiber filter.

The water was analyzed within several hours for reactive phosphate or frozen for later analysis. Reactive phosphate was measured colorimetrically using a molybdate, ascorbic acid reagent on a Technicon II Autoanalyzer (IIS method No. 155-71w); total phosphate was measured in the same manner after the water had been oxidized in a glass beaker with persulfate (Menzel and Corwin, 1965; Olsen, 1966). Phosphate concentrations were monitored continuously for some experiments by pumping incubation water continuously into the autoanalyzer.

Water samples for ^{32}P counting were also taken with a 50 ml syringe, filtered, and transferred into glass scintillation vials. The samples were counted on a Beckman LS100 Liquid Scintillation counter. These samples were counted with no addition of scintillation fluid. Light is emitted when particles (in this case electrons) travel faster than the speed of light in the medium (Cerenkov radiation, Ross 1976). Even though higher efficiency of ^{32}P counting could be obtained using liquid scintillation techniques, Cerenkov counting was used to minimize isotope handling, quenching problems, and cost. The counting efficiency of this technique was approximately 25%, as opposed to liquid scintillation counting of approximately 90-100%. The standard curve is linear, demonstrating the absence of quenching problems when using this technique.

Respiration of the community was determined by monitoring the decrease in oxygen of the incubation water with a YSI 57 O_2 meter while the aquarium was in the dark. Temperature of the incubation water was always monitored and the aquarium placed in a cooling bath if necessary.

Results:

When the reef organisms were placed in the incubation aquarium, the initial low level phosphate reef water usually increased (Figure 2), suggesting that the organisms released or excreted phosphate to the surrounding medium. Equilibrium phosphate values in the aquarium (both RP and TP) were above the initial, low level phosphate concentrations of the ambient reef flat water. This was not true however for a dark incubation where phosphate decreased to an undetectable level (Figure 3). These communities took up phosphate rapidly after phosphate was added to the aquaria (Figures 2 and 3). Both reactive phosphate and total

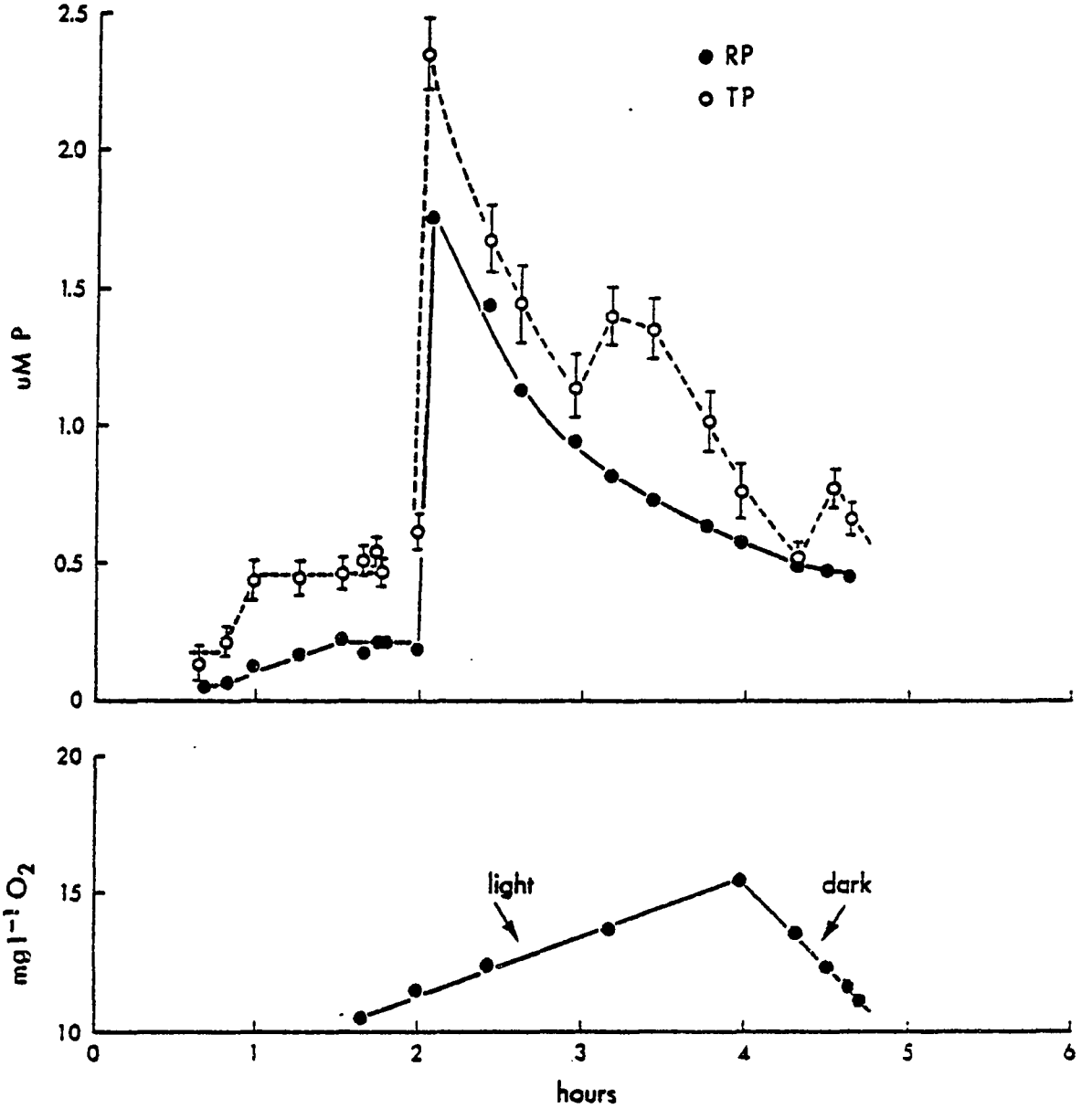

Figure 2: Phosphate concentration vs time and oxygen concentration vs time for an aquarium incubation of a mixed reef community in the light. Organisms were added to reef water prior to 1 hour, and phosphate (K_2HPO_4) was added at 2 hours.

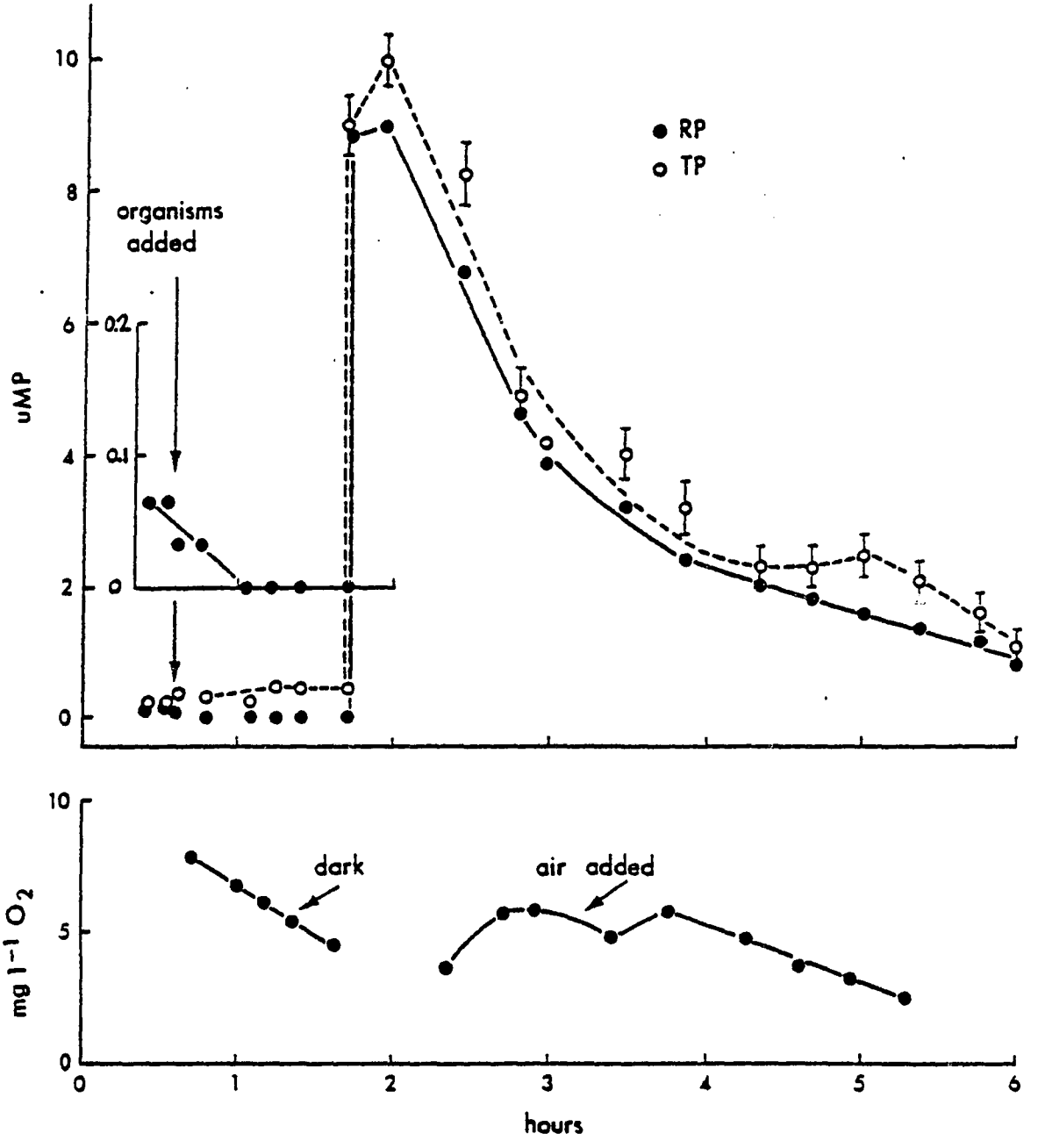

Figure 3: Phosphate concentration vs time and oxygen concentration vs time for an aquarium incubation of a mixed reef community in the dark. Organisms were added to reef water at 30 minutes and phosphate (K_2HPO_4) was added at 1 hour, 40 minutes. An air stone supplied oxygen to the incubation water.

phosphate decreased rapidly. Note however that the rate of uptake slowed down as concentrations approached the initial value. Total phosphate was always slightly higher than reactive phosphate. In some incubations total phosphate appeared to increase suddenly during uptake, even though the reactive phosphate did not increase (see Figure 2). Clearly, the communities can take up large amounts of phosphate.

The uptake of oxygen in the dark was linear with respect to time (Figure 2). This oxygen uptake rate (dark respiration rate) was used to normalize the phosphate uptake rates. Nutrient uptake rates are usually normalized to biomass. Since large complex communities were used in these uptake experiments, the community dark respiration rate was considered to be the best estimate of "metabolic biomass;" and, since oxygen fluxes are better known for reef communities than biomass, these data could be directly compared to field respiration rates. The respiration rates of these communities incubated in aquaria per unit area of aquarium were similar to respiration rates measured in the field per unit area of reef flat. Therefore, the biomass per unit area of aquarium was approximately the same as the biomass per unit area of reef flat. Temperature was held within $3^{\circ}C$ during these incubations.

The incubations of Figures 2 and 3 illustrate that these reef communities took up phosphate at high concentrations in the light or in the dark, however at low ambient phosphate concentrations, there appeared to be no uptake. To determine whether phosphate is exchanged (uptake and release) with the reef community at low phosphate levels, ^{32}P as orthophosphate was added to the incubation water. If uptake and release of phosphate occur continually (phosphate exchange), the labeled ^{32}P should be removed from the incubation water even though reactive and total

phosphate remain constant. The results to the ^{32}P incubations show that there was net excretion of phosphate by the sample communities (reactive and total phosphate increased during the course of the experiment) and that ^{32}P was removed from the water in an apparent exponential manner (Figures 4 and 5). Filtered and unfiltered water samples were taken to determine the phosphate scavenging ability of particles greater in size than 0.45 um suspended in the water. There was no significant difference of ^{32}P activity between filtered and unfiltered water samples. Therefore all particles greater than 0.45 um, including the plankton, do not significantly interfere with the uptake of ^{32}P by the benthos. The region labeled "sand" in Figure 5 will be discussed later.

The rates of phosphate uptake for high phosphate concentrations were determined by taking the initial change in reactive phosphate and normalizing, or dividing, by the dark respiration rate for that community.

$$\%P \text{ uptake} = \frac{\text{initial phosphate change}}{\text{time change}} \Big/ \frac{\text{oxygen change}}{\text{time change}} \times 100$$

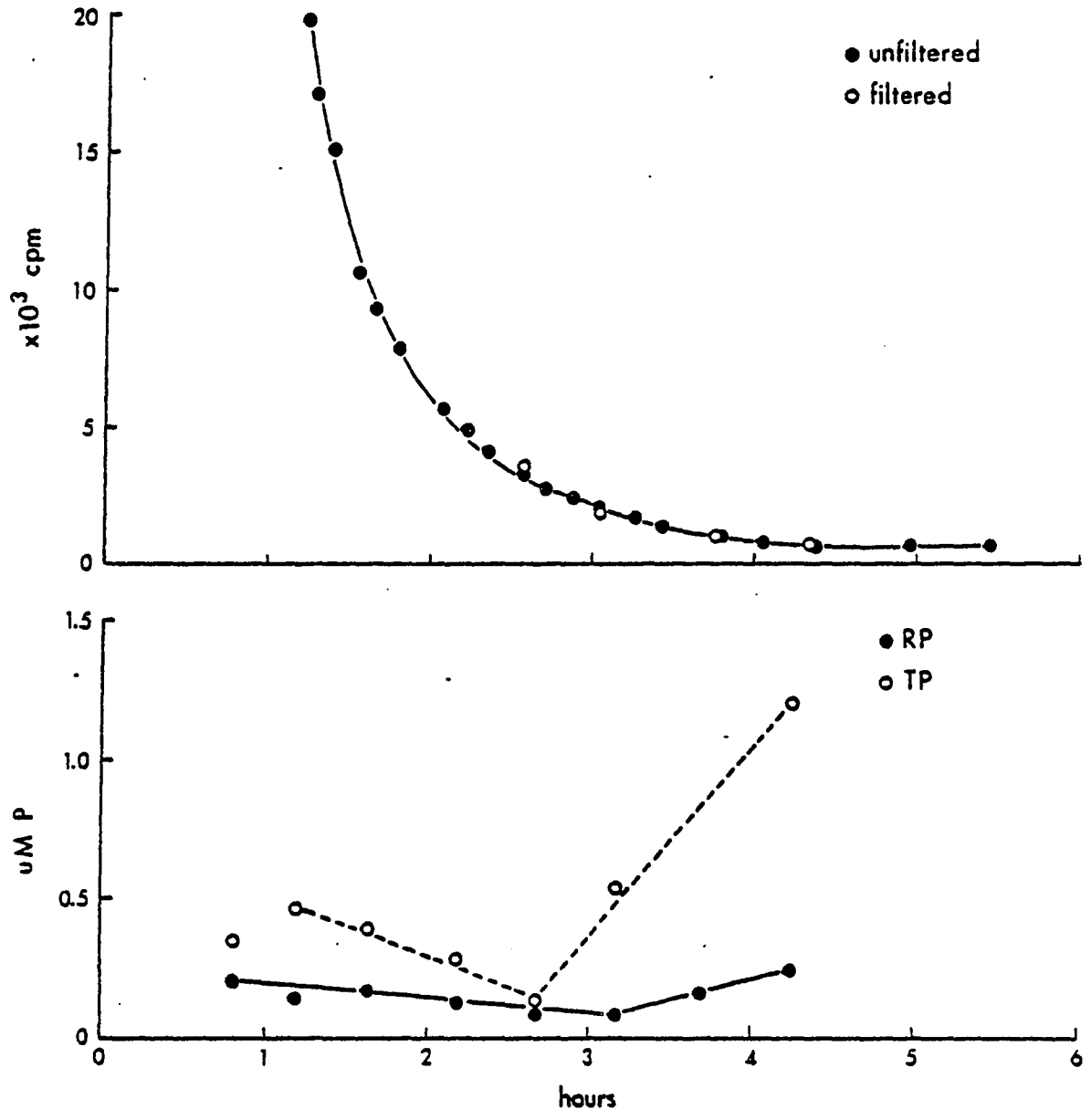

Figure 4: Cpm vs time and phosphate concentration vs time for ^{32}P uptake of a mixed reef community (experiment A). Water samples were filtered and unfiltered. Note the decrease in reactive phosphate (RP) and total phosphate (TP), then the increase during the incubation.

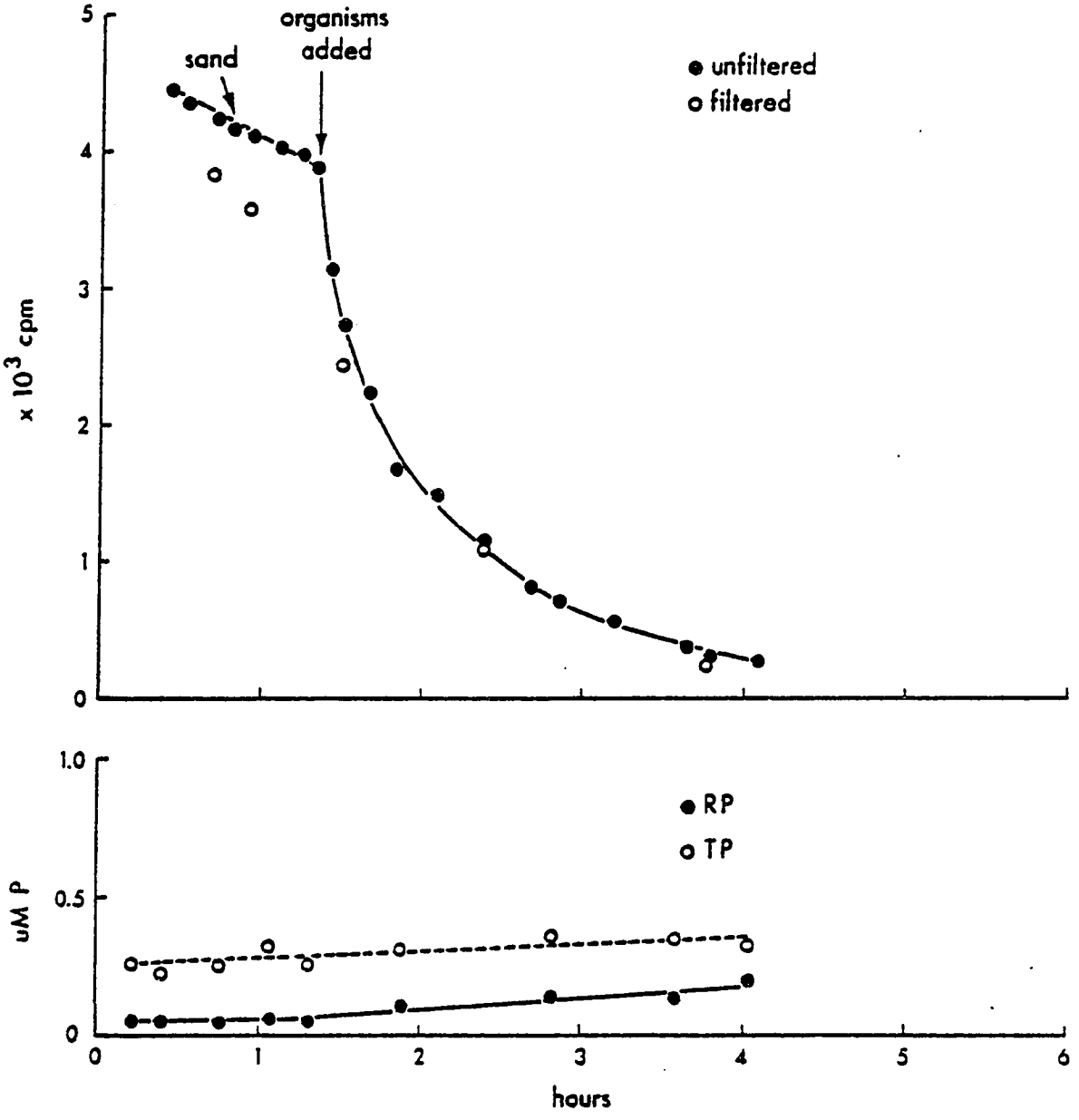

Figure 5: Cpm vs time and phosphate concentration vs time for ^{32}P uptake of sand and then a mixed reef community (experiment B). Water samples were filtered and unfiltered. Note the increase in reactive phosphate (RP) and total phosphate (TP) during the incubation.

The rates of phosphate uptake at low phosphate concentrations (concentrations found over the reef flat community) were calculated by solving for the uptake rate (K_2) in the following differential equations (Caperon et. al., 1979):

$$\frac{d^{31}P}{dt} = K_1 - \frac{K_2(^{31}P)}{(^{31}P + ^{32}P)} \quad (1)$$

$$\frac{d^{32}P}{dt} = \frac{-K_2(^{32}P)}{(^{31}P + ^{32}P)} \quad (2)$$

^{31}P = concentration of available ^{31}P

^{32}P = concentration of ^{32}P

K_1 = excretion rate of P

K_2 = uptake rate of P

Equation #1 is: the rate of change of unlabeled phosphate (^{31}P) equals the excretion rate of ^{31}P, minus the uptake rate times the proportion of ^{31}P to the total available P. Equation #2 is: the rate of change of ^{32}P equals the excretion rate of ^{32}P (in equation #2 it is assummed to be 0), minus the uptake rate times the proportion of ^{32}P to the total available P. Since the amount of ^{32}P is small compared to ^{31}P (the addition of ^{32}P does not change the level of reactive phosphate or total phosphate, see Figures 4 and 5), equations #1 and #2 can be simplified to equations #3 and #4 respectively:

$$\frac{d^{31}P}{dt} = K_1 - K_2(1) \quad (3)$$

$$\frac{d^{32}P}{dt} = \frac{-K_2(^{32}P)}{(^{31}P)} \quad (4)$$

Equation 3 states that the rate of change of ^{31}P is constant, and equation 4 states that the rate of change of ^{32}P is proportional to the ratio of ^{32}P to available ^{31}P. Equation 4 assumes that ^{32}P behaves as the available ^{31}P.

Analysis #1:

If the uptake rate K_2 remains proportional to ^{31}P ($K_2 = K^{31}P$), equation 4 can be reduced to:

$$\frac{d^{32}P}{dt} = \frac{-(K^{31}P)(^{32}P)}{(^{31}P)} = -K^{32}P \qquad (5)$$

Equation 5 integrated with respect to time (t) is:

$$^{32}P = ae^{-Kt} \qquad (6)$$

The natural log of equation 6 is a linear function of time (t):

$$\ln ^{32}P = \ln(a) - K t \qquad (7)$$

A semi-log plot of cpm vs time will be a straight line if: (1) K_2 is proportional to ^{31}P, and (2) ^{32}P behaves as ^{31}P. Semi-log plots for the two ^{32}P experiments show that for Experiment B the plot was linear (r^2 = .99; Figure 6) but less so for Experiment A (r^2 = 0.94, Figure 7). In Experiment A the uptake rate of ^{32}P slowed down during the last 1-2 hours of the incubation (Figure 7). This slow down in ^{32}P uptake means that one or both of the two conditions for linearity were violated: (1) K_2 did not remain in constant proportion to the available phosphate during this part of the experiment, or (2) the ^{32}P was not well-mixed in the available phosphate pool. I suggest that the rapid excretion of total phosphate introduced some available organic compounds which altered the uptake of orthophosphate, hence the ^{32}P (see Figure 4). To calculate the uptake rate K_2 from this analysis, K, the slope, was determined from the least squares regression of the log cpm vs time and multiplied by the mean reactive phosphate concentration (assuming reactive phosphate is biologically available phosphate). The calculated K_2 and mean reactive phosphate concentration for Experiment A is 0.11% of the respiration rate and 0.15 uM, respectively, and for Experiment B, 0.09% and 0.13 uM, respectively.

Analysis #2:

In the previous analysis it was assumed that K_2 was proportional to the concentration of reactive phosphate. The following analysis assumes K_2 is constant.

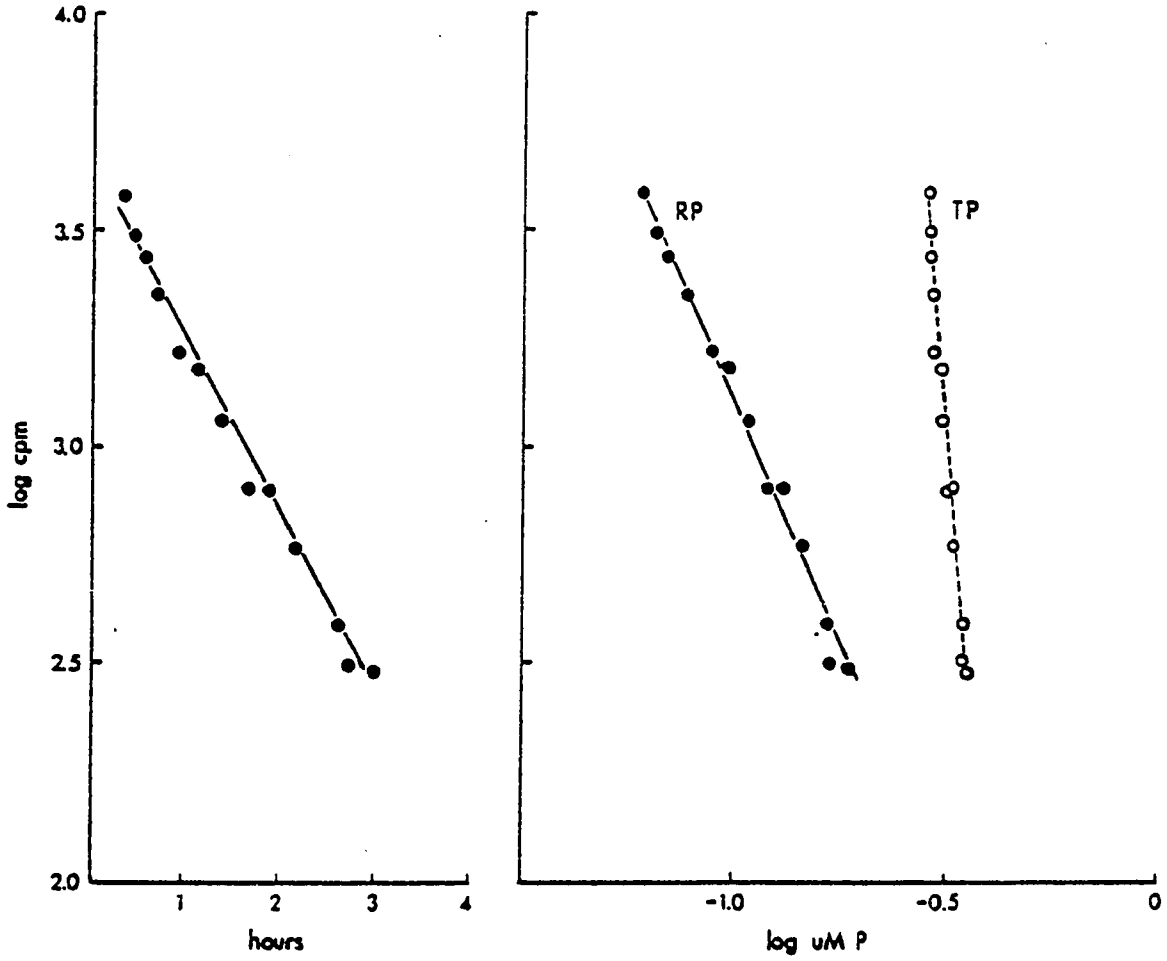

Figure 6: Log cpm vs time and log cpm vs log reactive phosphate (RP) and log total phosphate (TP) for the ^{32}P experiment B (see Figure 5).

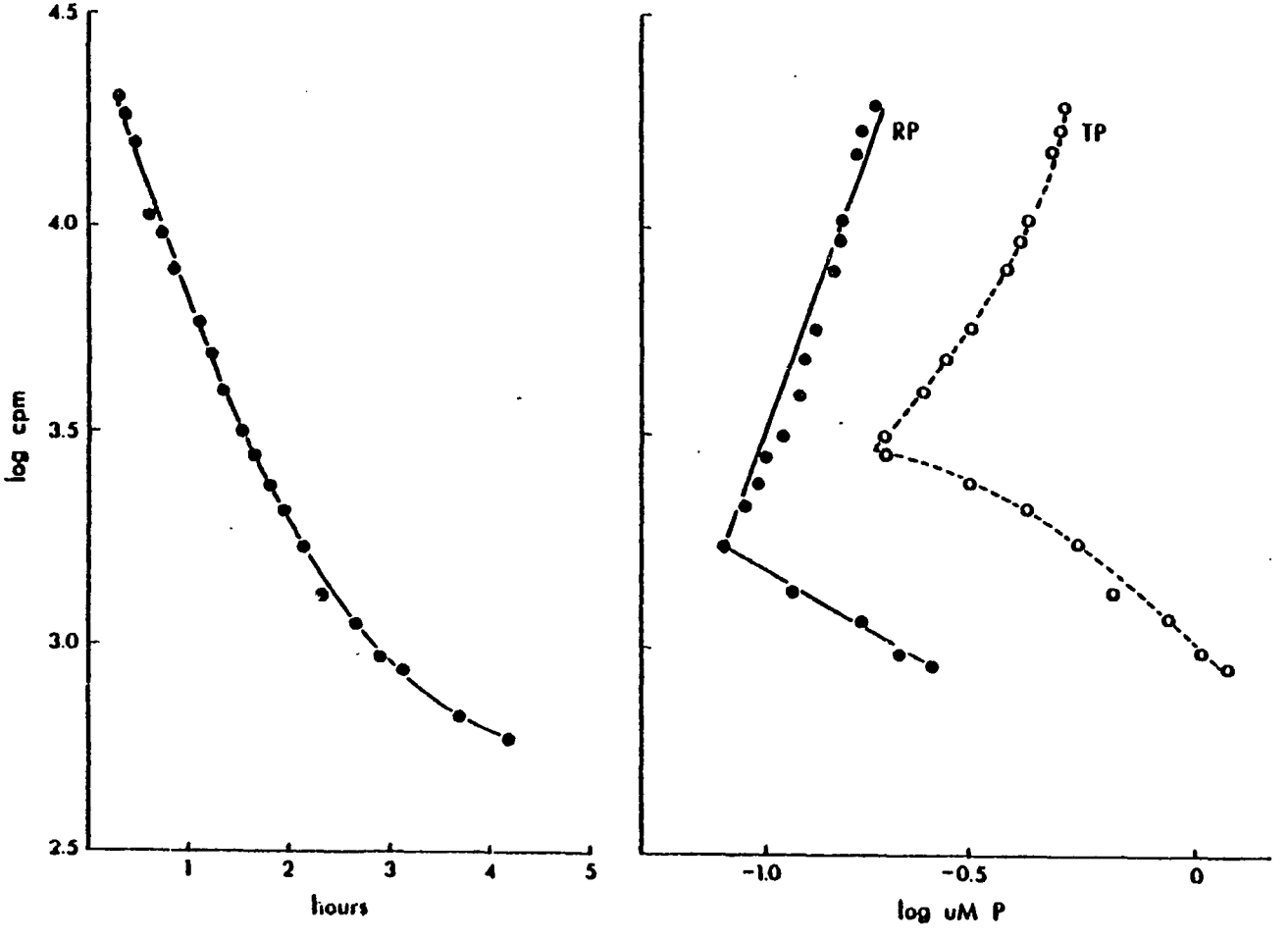

Figure 7: Log cpm vs time and log cpm vs log reactive phosphate (RP) and log total phosphate (TP) for the ^{32}P experiment A (see Figure 4).

Equation 4 was modified to include increasing and decreasing phosphate concentrations throughout the experiments (Figures 4 and 5). The increases and decreases in phosphate were fit to a linear function with respect to time:

$$^{31}P = {}^{31}P_o + (K_1 - K_2)t \qquad (8)$$

$^{31}P_o$ = starting concentration of P

t = time

Substituting equation 8 for ^{31}P in equation 4, equation 4 is modified to:

$$\frac{d^{32}P}{dt} = \frac{-K_2(^{32}P)}{(^{31}P_o + (K_1 - K_2)t)} \qquad (9)$$

Equation 9 states that the rate of change of ^{32}P in the incubation water is a function of the ratio between ^{32}P concentration and the changing ^{31}P concentration. Equation 9 can be further modified to:

$$\frac{d^{32}P}{^{32}P} = -K_2 \frac{dt}{(^{31}P_o + (K_1 - K_2)t)} \qquad (10)$$

and

$$d\ln {}^{32}P = \frac{-K_2}{(K_1 - K_2)} d\ln (^{31}P) \qquad (11)$$

By equation 11, the slope of the plot of log ^{32}P vs log ^{31}P is $-K_2/(K_1-K_2)$. The slope of ^{31}P vs time is (K_1-K_2). These two slopes, $-K_2/(K_1-K_2)$ and (K_1-K_2), multiplied together are $-K_2$, the uptake rate of phosphate.

To analyze the data in this manner the least squares regression line was fit through the reactive and total phosphate vs time data to get the best estimate of the slope (K_1-K_2) and the best estimates of ^{31}P at each time interval for both forms of phosphate. Calculated estimates of ^{31}P were used to plot the log cpm vs log ^{31}P so that the slope $-K_2/(K_1-K_2)$ could be calculated (least squares regression, type II). Figures 6 and 7 show plots of log cpm vs log reactive phosphate and log total phosphate for each experiment. Assuming that: (1) the uptake rate K_2 is constant, and (2) ^{32}P behaves as a well-mixed portion of available phosphate (^{31}P), then the plots of log cpm vs log reactive phosphate or log total phosphate should be straight lines if reactive phosphate or total phosphate respectively are proportional to available P (^{31}P). The plots can also be straight lines if change in K_2 is offset by change in the ratio of actual ^{32}P to available ^{31}P. The plots will not be straight lines if the above conditions are not met. In Experiment B, the uptake rate of ^{32}P did not appear to change and since the plots of log cpm vs log ^{31}P for both reactive phosphate and total phosphate were straight lines (Figure 6), it cannot be concluded which form of phosphate represented available phosphate.

However in Experiment A log cpm vs log ^{31}P was approximately linear for reactive phosphate and curvilinear for total phosphate (Figure 7). Therefore in Experiment A reactive phosphate met the above conditions better than total phosphate.

Results of Experiment A suggest that available phosphate (^{31}P) is approximated by or proportional to the reactive phosphate pool, and not the total phosphate pool. This is not conclusive, however, since change in K_2 as the phosphate concentration changed could have created curvilinearity. The uptake rates K_2 were calculated using the slope for the reactive phosphate data (K_1-K_2) and the slope of the log cpm vs log reactive phosphate $-K_2/(K_1-K_2)$ as described earlier. K_2 for the first two hours of Experiment A (Figure 7) is 0.13% of respiration rate, and the last two hours, 0.09%. K_2 for Experiment B was calculated as 0.09%, the same as with analysis #1.

The assumptions of these two analyses seem to contradict each other, that is in the first analysis K_2 is proportional to concentration and in the second analysis K_2 is held constant. Since the calculated values of K_2 are so close for each analysis, the reasonable interpretation is that any changes in K_2 are within the error of this analysis. Analyses 1 and 2 yield the same uptake rates for Experiments A and B.

The semi-log plot of cpm vs time for Experiment A shows that the ^{32}P uptake slowed down. If it is assumed that K_2 remained constant throughout the experiment, then the linear relationship between log cpm and log reactive phosphate during the last part of this incubation suggests that ^{31}P remained proportional to reactive phosphate (Figure 7). I suggest that the original assumption was violated, ^{32}P orthophosphate was not representative of all the available phosphate. Available organic phosphate compounds from the rapid release of total phosphate might have influenced the uptake of orthophosphate (see Figure 4). In general however the above two ^{32}P experiments suggest that ^{32}P behaved as a well-mixed portion of the reactive phosphate pool.

The results to these calculations indicate that the uptake rate of phosphate at low phosphate concentrations is about 0.1% of the community respiration rate.

The uptake rates of reactive phosphate normalized to the respiration rate (mole P uptake/mole O_2 respired x 100; see earlier discussion) for all experiments are listed in Table 1. A plot of these data, Figure 8, shows that the uptake rate of phosphate is a function of the phosphate concentration. The observed relationship can be described as a hyperbolic relationship (non-linear least squares fit). At the concentrations below about 10 uM, however, the relationship between uptake rate and concentration is linear. In fact the environmentally meaningful concentrations, those below about 2 uM, are linear (r^2 = .99), suggesting that the uptake rate is proportional to the concentration of reactive phosphate. From these limited data the predicted phosphate uptake rate as a percentage of respiration rate for any concentration of phosphate is:

% uptake rate = 0.58 (P) + .013

P = uM P

If the above relationship is correct then the assumption that K_2 remained constant in the ^{32}P experiments is not valid, and Analysis #1 would be the correct mathematical analysis.

B. Alkaline Phosphatase Experiments.

Alkaline phosphatase is a cell surface enzyme which catalyzes the hydrolysis of a variety of phosphate esters. It typically can cleave phosphate from organic bonds (C-O) or other phosphate groups. The enzyme is usually found in cell walls of algae and cell membranes of unicellular organisms (Kuenzler and Perras, 1965; Torriani, 1960). The enzyme

Table 1. -- Experimental parameters for phosphate uptake experiments

Experiment (date)	Aquarium Volume (l)	Area (m^2)	Respiration Rate (μmoles O_2 min^{-1})	% Initial Uptake Rate (μmoles P min^{-1} per μmoles O_2 min^{-1})	Initial P Concentration (μM)
7/29/80 (A)	9	0.07	16.4	0.11	0.15
8/1/80 (B)	7	0.07	15.8	0.09	0.13
8/14/80	9.9	0.07	26.9	0.7	1.2
9/19/80	5	0.04	7.0	1.3	2.2
7/21/80	17	0.13	35.4	1.5	3.9
8/21/80	11.3	0.13	21.7	4.3	6.3
9/11/80	9.1	0.07	13.0	5.6	20.5
7/14/80	14	0.13	39.0	5.3	46.0

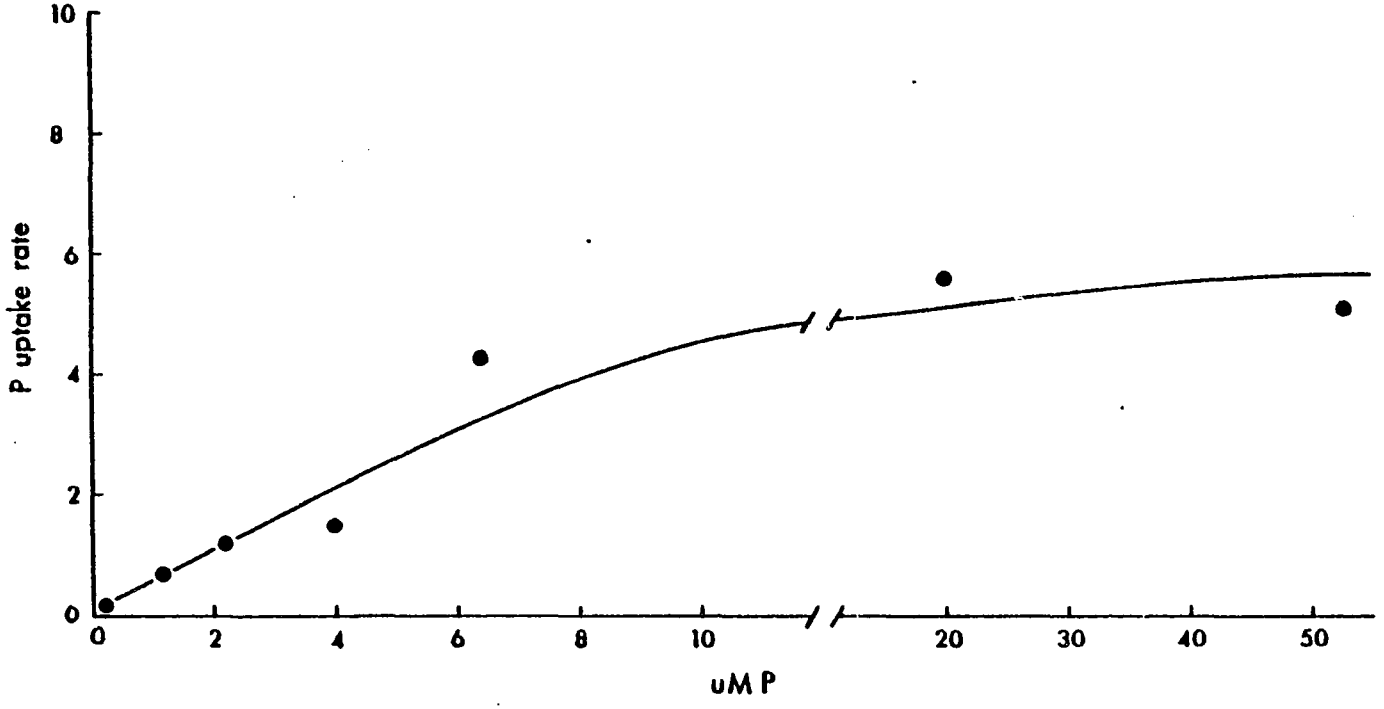

Figure 8: Phosphate uptake rate per respiration rate (moles P uptake/ moles O_2 respired x 100) vs phosphate concentration. Note the change in phosphate concentration scale.

generally shows increased activity when unicellular organisms are phosphate deficient (Kuenzler and Perras, 1965; Bone, 1971). Since coral reef ecosystems generally reside in water of low phosphate concentration, it seemed reasonable to evaluate the ability of the reef community, through the activity of alkaline phosphatase, to obtain orthophosphate from organic compounds in the water.

Methods:

The activity of alkaline phosphatase was measured using para-nitrophenyl phosphate (p-NPP) as a dissolved organic substrate. When p-NPP loses its phosphate and becomes paranitrophenol (p-NP), the solution turns yellow. Therefore the activity of the enzyme is measured by following the color development of the solution (see Kuenzler and Perras, 1965 for a detailed procedure). The initial rate of color development is a function of the enzyme concentration when the substrate (p-NPP) is not limiting. Preliminary experiments showed that p-NPP is measured as total phosphate, and then when it is enzymatically cleaved to p-NP, the orthophosphate remains in solution as reactive phosphate. It is assummed that all measured activity is due to "alkaline phosphatase", although I recognize that p-NPP can be hydrolyzed by other enzymes.

The working solution of p-NPP is: 1mM p-NPP, 1M Tris pH 8.0; and 0.01 M $MgSO_4$ (Sigma Chemical Co.). A "unit" definition (per Sigma) is the amount of enzyme which will hydrolyze 1 umole of p-NPP per minute at pH 10.4, at 37°C. The enzyme activity assayed at 37°C, pH 10.4, is approximately equal to the activity determined at 25°C, pH 8.0 (Sigma). Experiments indicated that the hydrolysis of 1mM p-NPP to p-NP does not significantly alter the pH of seawater; and further there is ample Mg and SO_4 in seawater to stabilize the enzyme reaction. I assayed for alkaline

phosphatase in a working solution of 0.1 - 1.0 mM p-NPP in seawater at about 25°C. This procedure was compared to the standard procedure using commercially available enzyme (Sigma). Over a large range of enzyme activities the seawater procedure showed a mean activity of 0.62 of the Sigma procedure. All activities measured using the seawater procedure were converted to standard Sigma activity units.

In the following experiments reef material was collected from the Kaneohe Bay barrier reef flat and placed in an aquarium (as in the exchange experiments). p-NPP was added to the aquarium to bring the total incubation water (water taken from the reef flat) to 0.1 mM p-NPP. Several samples of this initial incubation water were held as control samples. The aquarium filled with organisms was allowed to sit for several hours, and the yellow color development of the incubation water was followed spectrophotometrically.

All absorbances were plotted; the best straight line visually fit through the linear part of the curve, and an initial rate of color development calculated. Control rates were subtracted from the experimental rates. The rate of color development was then converted to umoles of p-NPP hydrolyzed per minute. One mole of p-NP is 1.62×10^4 absorbance units.

Results:

During the incubation of the reef organisms, total phosphate decreased in the incubation water while p-NP and reactive phosphate increased (Figure 9). Since total phosphate decreased, the reef community clearly took up phosphate from the p-NPP. The uptake rate of phosphate from the organic substrate was high, approximately 5.3% of the

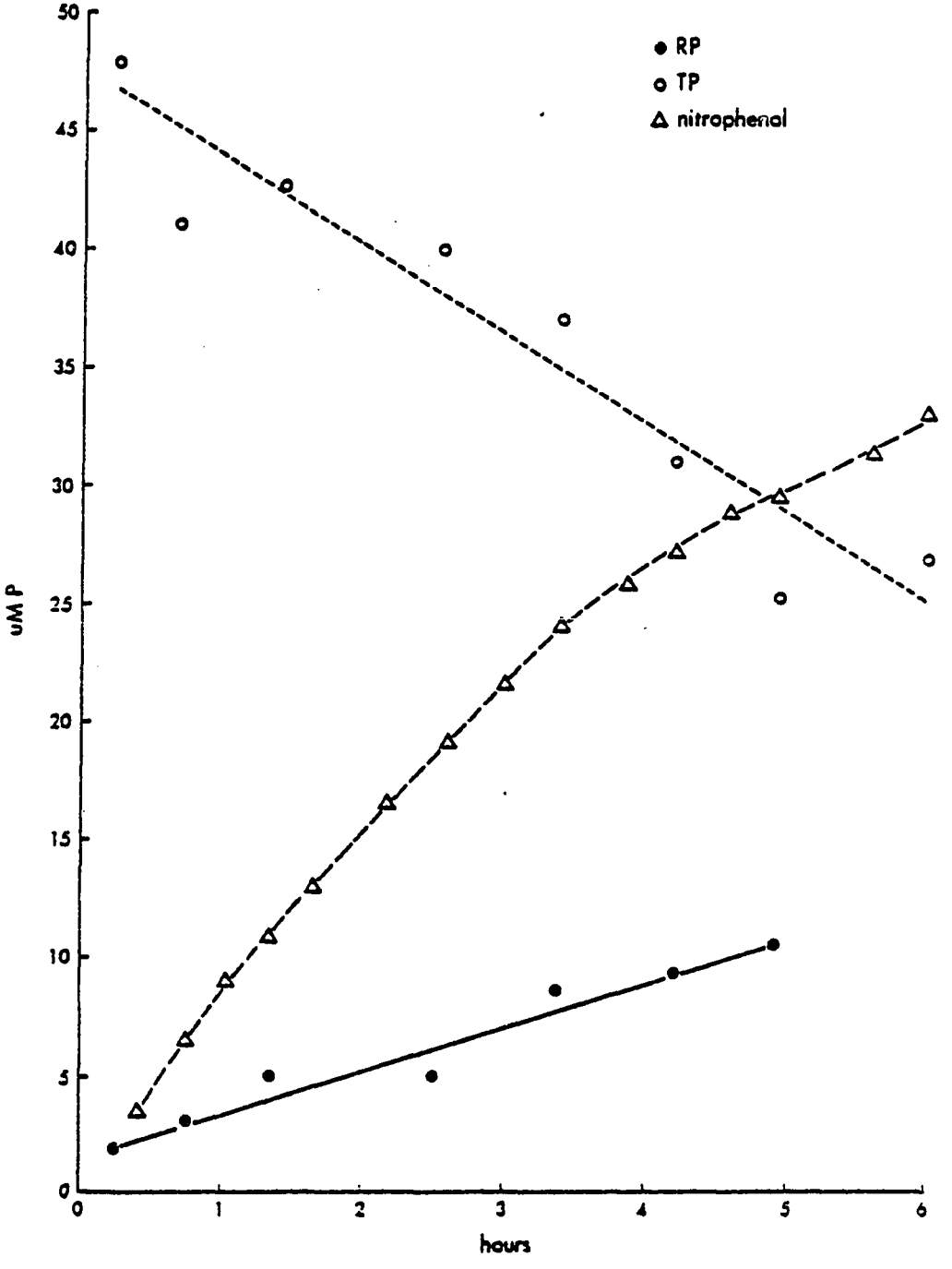

Figure 9: Total phosphate, reactive phosphate, and phosphate equivalent para-nitrophenyl concentration for an aquarium addition of para-nitrophenyl phosphate. Note that the reactive phosphate increases linearly and the uptake of para-nitrophenyl phosphate is curvilinear.

respiration rate. This high uptake rate is about the same as the uptake rates for reactive phosphate at concentrations of reactive phosphate greater than 10 uM. The available phosphate substrate in this experiment was the concentration of the p-NPP, or about 50 uM. Therefore at abnormally high concentrations of phosphate, the uptake ability of the reef is about the same for orthophosphate as it is for mono-ester bonded phosphate. The curvilinear feature of p-NP (Figure 9) is typical of enzyme kinetics, and demonstrates that the rate of uptake was a function of concentration for the organically bound phosphate. The uptake ability of the reef community at low concentrations of organically bound phosphate cannot be determined from this experiment; however, this experiment shows that the reef community can take up phosphate from an organic substrate.

Samples of reef substrata collected from Enewetak Atoll, Marshall Islands, also showed relatively high alkaline phosphatase activity. The activity of this enzyme seems common. The Enewetak alkaline phosphatase activities per unit surface area for small reef subsamples (0.01 m^2) were approximately the same as the activity per unit surface area for Kaneohe Bay large samples (0.1 m^2); (0.86 mmoles $m^{-2}hr^{-1}$ vs 0.88 $m^{-2}hr^{-1}$). The data from Enewetak suggest that surfaces with heavy epiphytic communities have higher alkaline phosphatase activity per gram dry weight of reef material than surfaces without epiphytic communities. Further experiments with Lyngbia majuscula showed that alkaline phosphatase activity did not differ in P-starved, or N-starved batch cultures. Since other works have demonstrated that alkaline phosphatase activity usually increases when the cells have been starved for phosphate (Bone 1971), the

results to the culture experiment suggest that Lyngbia majuscula might have already been starved for phosphorus.

The important result from this work is that the enzyme alkaline phosphatase allows the community to take up phosphate from organic phosphate compounds. The total phosphate measured in water over the reef flat might have some biologically available organic phosphate compounds. These compounds are either directly hydrolyzed to orthophosphate or taken up through the activity of alkaline phosphatase. Even though alkaline phosphatase activity appears to be common on the surfaces of coral reef substrata, I cannot state that the presence of this enzyme on reef substrates implies phosphate limitation of the reef community. These enzyme activities must be normalized to biomass, or better, to some metabolic parameter before statements can be made as to phosphate limitation for the whole community.

C. Adsorption

Phosphate readily adsorbs to sediment minerals and organic material (Shuka et. al., 1971; Rodel et. al., 1977; Simkiss, 1964). Therefore the phosphate uptake rate measured in the previous experiments might be heavily influenced by non-biological reactions, particularly physical adsorption to the substratum. Several experiments were designed explicitly to test whether adsorption was significant.

1. Nucleic Acid Experiments:

The first experiment to be discussed ascertains that phosphate gets into cellular components during a short term ^{33}P incubation. ^{33}P is a lower energy isotope of phosphorus than ^{32}P. ^{32}P can be counted in water without scintillation fluid (Cerenkov counting) whereas ^{33}P has an energy spectrum similar to ^{14}C and therefore requires liquid scintillation fluid. The half-lives of ^{32}P and ^{33}P isotopes are similar. This experiment involved incubating small subsamples of reef producers in ^{33}P orthophosphate. The activity of ^{33}P was then measured in the nucleic acid pools of these organisms.

Methods:

Reef material was collected and brought to the laboratory where it was maintained in an aerated aquarium. The next day, small (0.1 - 0.2 cm^3) pieces of the substrata were broken off and put in a 1 liter beaker. Subsamples of coralline algae, coral, rubble, filamentous algae, and thalloid algae were included in the experiment. 10 uCi ^{33}P were added to 300 ml of reef water. The reef material was sampled after approximately 1 hour and 3 hours to determine the amount of ^{33}P in the cellular nucleic acids. Samples were then placed in 5 ml of boiling 60 mM K_2HPO_4 buffer, pH 7.3. This step solubilized orthophosphate, sugar phosphates, nuceotides, and some nucleic acids. A 1 ml sample of this solution was frozen for ^{33}P counting. Enough tricholoric acetic acid (TCA) and HCl were added to the remaining solution to bring the final solution to 6% TCA and 1 M HCl. The $CaCO_3$ substratum was allowed to dissolve, pH checked to insure it to be near 1, and then the solution frozen for nucleic acid extraction. To insure nucleic acid precipitation in the acidic solution 1 mg of RNA, 1 mg of DNA, and celite were put in the test tubes. The

remaining pellet, containing precipitated nucleic acids, was resuspended three times with 5% ICA at 4^{o} C. This insures complete removal of contaminating labeled phosphate compounds. The pellet was then washed two times with 95% ethanol at 4^{o} C. The ethanol was evaporated and then the pellet extracted for nucleic acids in boiling 5% TCA. This solution was centrifuged and ½ ml of the supernatant counted for ^{33}P activity with a Searle Delta 300 liquid scintillation counter. 3 mls of aquasol were used as the liquid scintillation fluid. The ^{33}P was counted in the ^{14}C window and the ^{3}H window; a channels ratio was used to adjust all samples for quenching.

Results:

The results of this experiment indicate that ^{33}P, after removal from the incubation water, was incorporated into the nucleic acid fraction of the cellular phosphate. Table 2 lists the activity (dpm) found in the 60 mM K_2HPO_4 buffer extracted fraction and the nucleic acid fraction for the 10 different reef samples for the 1 hour and 3 hour sampling period. The biomass of the 3 hour sampling period was 20-30% of the 1 hour sampling period. Note however that the activity of ^{33}P generally increased in the nucleic acid pool, even though the biomass of these samples was lower. The nucleic acid pool is 6.6% of the 60 mM PO_4 extracted pool for the 1 hour sampling, and 20.4% for the 3 hour sampling. These percentages suggest that the nucleic acid pools accumulated phosphate relative to the labile phosphate pools. These results confirm qualitatively that the rapidly exchanged phosphate got into cellular phosphate pools, and was not just adsorbed to the surfaces of the reef community.

Table 2. — Dpm (^{33}P) in two intracellular pools of phosphate for a variety of reef producers. The 60 mM PO_4 extractable pool represents an unknown fraction of adsorbed phosphate, intracellular ortho-phosphate, and low molecular weight intracellular phosphate compounds such as sugar phosphates and nucleoside phosphates.

Reef Material	70 Minute dpm		200 Minute dpm	
	60 mM PO_4 Extractable	Nucleic Acids	60 mM PO_4 Extractable	Nucleic Acids
Filamentous green	2859	165	251	73
Lygnbia	4522	172	1117	116
Hypnia	536	98	1636	303
Dictyota	514	60	138	32
Halomedia	136	24	80	38
Coralline	1567	117	432	116
Coralline	351	24	165	51
Coralline	271	30	472	82
Rubble	249	54	236	122
Coral	1136	55	461	88
Total	12141	799	4988	1021
Mean	1214	80	499	102

2. High surface area, low respiration rate communities:

Another way to determine to what extent adsorption-desorption reactions influenced the ^{32}P exchange experiments of section A was to measure the uptake rate and release rate of phosphate from communities with high surface area and low respiration rate. It was reasoned that the high surface area of the community would favor adsorptive-desorptive reactions and the low respiration rate, or low biomass, would not favor biological exchange of phosphate.

Methods:

The methods of collection, transportation, incubation, and analysis for ^{32}P, reactive and total phosphate in these experiments were the same as they were in the exchange experiments (section A).

Results:

Sand was chosen as a high-surface area, low respiration community. The results of a ^{32}P uptake experiment (Figure 5) showed that at the same phosphate concentration the uptake rate of ^{32}P per respiration rate for sand was comparable to that for whole communities (sand/community = 1.1). Even with high surface area, the uptake rate of sand normalized to respiration rate is similar to a complex community; this similarity suggests that physical adsorption is small (less than 10%) compared to biologically mediated uptake of ^{32}P.

Another observation is worth mentioning. In the two ^{32}P uptake experiments (Figures 4 and 5), the sides of aquaria and the organisms were counted with a hand-held pan counter immediately after the incubation. Background counts at HIMB were about 10 cpm on this instrument. The sides of the aquaria showed an activity of 100-200 cpm, suggesting adsorption of ^{32}P onto the glass. The organisms however all indicated an activity of

50,000 - 100,000 cpm. The surfaces of the organisms showed a much higher ability to scavenge ^{32}P than the glass walls of the aquaria.

In another aquarium experiment, the organisms living in or on sand were killed within minutes after the addition of mercuric chloride. In this experiment, phosphate increased in the incubation water immediately after the addition of mercuric chloride, demonstrating that the organisms retain phosphate within the sand. Further experiments with dead reef communities in aquaria showed that the communities always showed a release of phosphate when poisoned with mercuric chloride or formaldehyde and could not take up any phosphate even at elevated phosphate concentration (Table 3). The release rates of phosphate measured in these poison experiments were 10-30 times faster than the release rates measured for the organisms living at ambient phosphate concentrations. Even if adsorption-desorption reactions occurred in these experiments, adsorption cannot take up all the biologically retained phosphate.

Reef substratum was ground to a fine powder and placed in seawater. All substrata showed a release of phosphate into seawater. The surfaces of coral and rubble (where most living cells are located) showed a greater release of phosphate than the insides of more inorganic portions of these substrata (Table 4). These extractions were also done in 0.5 M $NaHCO_3$, pH 8.3. Since HCO_3 has the ability to replace PO_4 on mineral sites (Olsen et. al., 1954) extractions with $NaHCO_3$ showed higher release of phosphate from the substrata than extractions with seawater (Table 4). H_2SO_4 extracted phosphate was even greater than $NaHCO_3$ extracted phosphate.

I conclude from these experiments that physical adsorption-desorption reactions are not responsible for the observed uptake of phosphate by the experimental communities; I suggest that the substratum

Table 3. — Phosphate release from dead sand (A) and a dead reef community (B).

Time (min)	O_2 (mg l^{-1})	RP (µM)	TP (µM)	Comments
A. MERCURIC CHLORIDE KILL OF SAND				
0		0.16		incubation reef water
10		0.09		
15		0.09		
20		0.13		add sand
30		0.09		
40		0.16		
45		0.19		add mercuric chloride
60		0.25		
80		0.56		
85		4.06		add K_2HPO_4
110		4.29		
130		4.65		
170		7.61		
205		8.20		
220		9.08		
250		9.85		
265		10.79		
B. FORMALDEHYDE KILL OF A REEF COMMUNITY				
0		0.02	.43	incubation reef water
25		0.07	.36	
42	5.6			respiration rate = 7.6
60	4.5			µmoles O_2 min^{-1}
70	4.0			
110	2.3			
135	1.8	0.14	.29	add formaldehyde
175	1.9	3.8	4.5	release rates:
180	1.5	4.0	4.9	initial = 6.9%
285	1.8	9.0	13.0	(µmoles P/µmoles O_2)
340	2.0	10.3	11.8	middle = 3.7%
1390	2.5	25.2		
1480	3.1	25.4	36.4	
1500	3.1	25.4	38.1	final = 1.9%

Table 4. -- Phosphorus extracted from coarsely ground rubble and coral samples. Amounts are μmoles P g^{-1} substratum.

Substrata	Extraction μmoles P g^{-1}		
	Seawater	$NaHCO_3$ (n=2)	H_2SO_4 (n=3)
Rubble			
surface	1.4	4.2	12.9
inside	.1	1.6	17.4
Coral			
surface	2.3	2.9	14.5
inside	.7	1.4	7.6

has already adsorbed its maximal amount of phosphate. Organisms require metabolic energy to retain phosphate in the reef. Adsorptive-desorptive reactions are negligible compared to the biological transfers of phosphate.

D. Field Data

Nutrient data over the Kaneohe Bay barrier reef flat were collected for a year (includes day and night) to determine whether phosphate is taken up by the reef community. If so, can it be scaled to carbon and used as a measure of net community production? The Kaneohe Bay barrier reef is a particularly good reef flat to measure changes in reactive phosphate, because it is wide and the flow of water over the reef is slow. The water resides over the reef benthos a long time compared to typical barrier reef flats.

Methods:

Water was collected from the ocean or the reef flat in a bucket and immediately sampled with a 50 ml syringe. The water was then filtered by forcing the water out of the syringe through an in-line 0.45 um GFC glass fiber filter and into a PVC sampling bottle. These water samples were taken back to the lab (HIMB) within several hours, frozen or directly run on a Technicon II Autoanalyzer for nutrients. The colorimetric reactions for nutrient determinations were standard Technicon methods (Technicon 155-71W). Total phosphate was determined by oxidizing the sample with persulfate (0.1% total solution by weight, heated for one hour, Menzel and Corwin, 1965) then run for reactive phosphate on the autoanalyzer. Oxygen was measured in the bucket with a YSI 57 O_2 meter, air calibrated at sealevel. Alkalinity and pH were determined by the techniques described

by Marsh and Smith (1977). The sampling was conducted in several manners. Water typically flows from the ocean over the reef flat into the lagoon (Figure 10). Bathen (1968) reports current speeds of 0-9 cm s^{-1} (mean = 6 cm s^{-1}) over the reef flat. I have also measured a mean current speed using dye patches and drogues of 6 cm s^{-1} in one meter deep water. These currents are slow enough to be affected by the wind and the tide conditions. Southerly wind can drive water from the lagoon and out into the ocean (observed 12-13-79). The tide also can affect the water mass transport over the reef. During high surf conditions water impinges on the fore-reef and moves laterally, creating small rip currents between the breakers. My sampling scheme was wide scale to reduce the variations created by these current conditions, and all data near the boundary between the ocean and the reef flat water are interpreted with caution.

Results:

Nutrient data for an entire year are summarized in Table 5. Samples collected in water deeper than 2 meters were considered "ocean" and those from 2 meters and shallower were considered "reef". The means and 95% confidence limits are reported for all data summed over the entire year. The results indicate that both reactive phosphate and total phosphate are significantly lower over the reef, and that the differences (reef - ocean) for reactive phosphate and total phosphate are not significantly different from each other (see Table 5). Ammonia showed a significant increase over the reef for the year mean. Nitrate indicated both uptake and release over the reef. For a repeated sampling at a single location, 6-23-80, both nitrate and ammonia indicated a significant release from the reef.

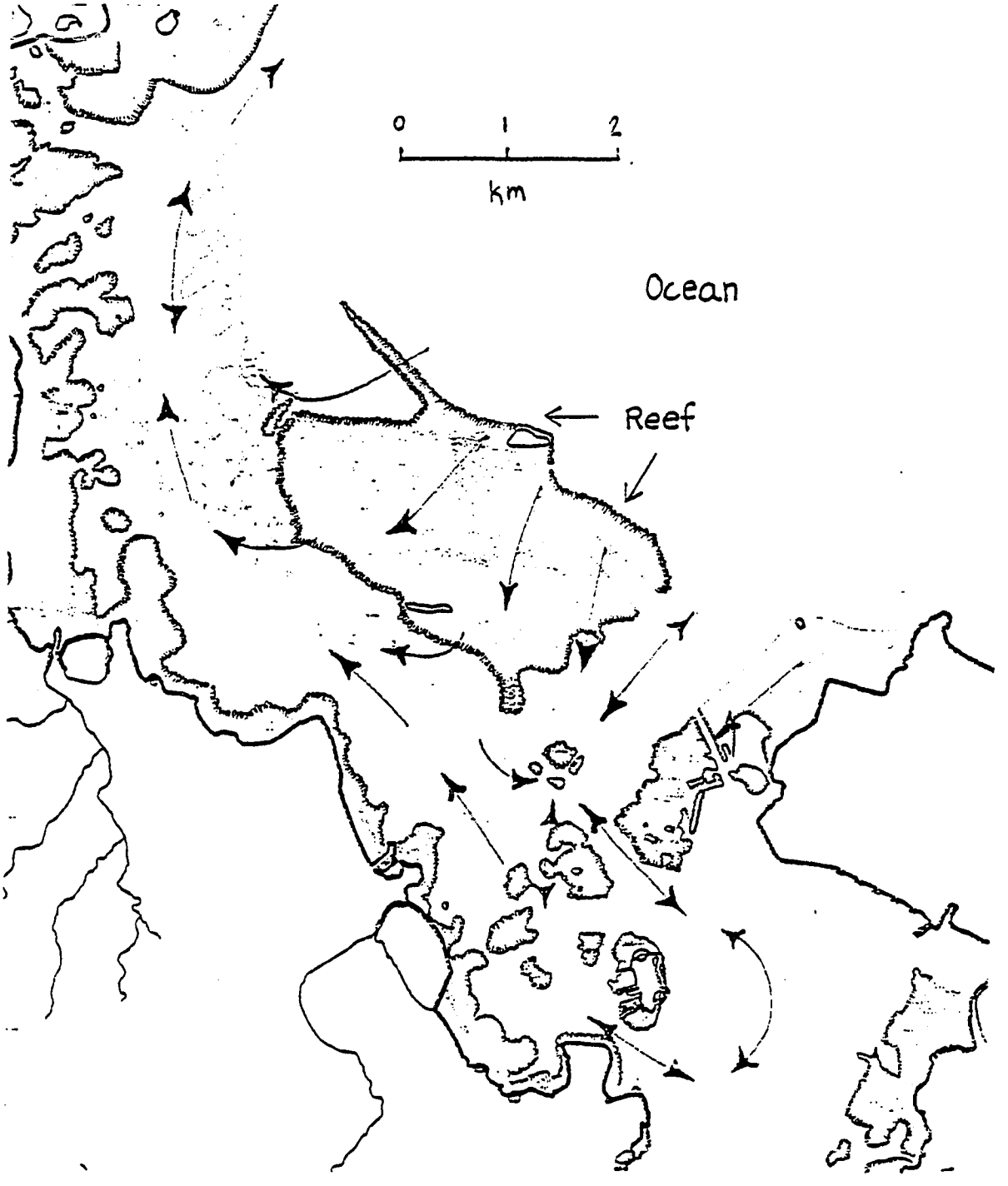

Figure 10: Current patterns over the Kaneohe Bay barrier reef.

Table 5. -- Nutrient data for Kaneohe Bay barrier reef. (n) mean ± 95% confidence limits. Water samples collected in water deeper than 2 meters are considered "ocean," and those collected in water shallower than 2 meters are considered "reef." "D" is the difference between reef and ocean (reef-ocean). Differences (D) labelled with "*" denotes that the ocean and reef means are significantly different.

Date	RP	TP	NO_3	NH_3	TN
9/12/79					
ocean	(31) .060±.016				
reef	(41) .032±.010				
D	-.028*				
9/14/79					
ocean	(5) .065±.006				
reef	(4) .011±.005				
D	-.054*				
9/18/79					
ocean	(5) .188±.195	(5) .465±.135	(5) .100±.118		(5) 5.036±1.475
reef	(13) .087±.031	(8) .389±.088	(8) .035±.018		(8) 5.115± .403
D	-.101	-.076	-.065		
12/11/79					
ocean	(6) .053±.025				
reef	(14) .014±.006				
D	-.039*				
12/13/79					
ocean	(14) .117±.009		(14) .317±.098		
reef	(18) .092±.011		(18) .296±.112		
D	-.025*		-.021		
3/2/80					
ocean	(12) .127±.027	(12) .371±.038	(12) .082±.059	(12) .097±.074	
reef	(8) .099±.026	(8) .311±.026	(8) .142±.101	(8) .201±.170	
D	-.028	-.060	.060	.104	

Table 5. -- (Continued) Nutrient data for Kaneohe Bay barrier reef

Date	RP	TP	NO_3	NH_3	TN
6/23/80					
ocean	(15) .102±.018	(8) .262±.055	(10) .027±.030	(10) .085±.029	
reef	(10) .042±.009	(10) .278±.022	(19) .225±.032	(10) .378±.0	
D	-.060*	.016	.198*	.293*	
6/24/80					
ocean	(5) .136±.047		(5) .217±.202	(5) .367±.410	
reef	(5) .056±.021		(5) .049±.058	(5) .086±.053	
D	-.080*		-.168	-.281	
7/21/80					
ocean	(5) .098±.0	(5) .207±.107	(5) .068±.079	(5) 0 ± 0	
reef	(5) .059±.017	(5) .118±.079	(5) .027±.076	(5) 0 ± 0	
D	-.039*	-.089	-.041	0	
8/23/80 (day)					
ocean	(5) .077±.016	(5) .234±.065			
reef	(15) .016±.014	(15) .274±.035			
D	-.061*	.040			
8/23/80 (night)					
ocean	(3) .057±.0	(3) .286±.171			
reef	(17) .005±.006	(17) .284±.046			
D	-.052*	-.002			
10/4/80 (day)					
ocean	(13) .095±.008		(13) .218±.030	(13) .477±.079	
reef	(23) .041±.007		(23) .175±.051	(23) .560±.067	
turf	(23) .054±.014		(23) .271±.022	(23) .903±.185	
seagrass	(33) .036±.009		(33) .123±.016	(33) .722±.100	
D	-.054*		-.043	.083	

Table 5. -- (Continued) Nutrient data for Kaneohe Bay barrier reef

Date	RP	TP	NO_3	NH_3	TN
10/4/80 (day)					
ocean					
reef	(18) .030±.013		(18) .157±.043	(18) .684±.089	
turf	(25) .057±.010		(25) .259±.033	(25) .850±.098	
seagrass	(21) .020±.010		(21) .113±.007	(17) .885±.080	
D	-.065*		-.061	.207*	
All 1979-81					
ocean	(117) .093±.006	(38) .314±.023	(67) .200±.023	(49) .214±.031	(5) 5.036±1.475
reef	(304) .004±.003	(63) .284±.017	(207) .176±.011	(178) .638±.031	(8) 5.115± .403
D	-.049*	-.030*	-.024	.424*	.079
95% limits of D	±.006	±.030			

The phosphate data are presented in another manner. All data are plotted according to the location where they were collected (Figures 11 and 12). These figures illustrate that lower phosphate values were found over the reef flat than in the ocean. For reactive phosphate data that were collected along a transect from ocean to lagoon, the data are plotted along this transect (Figure 13). The data are averaged for each 100 meter interval, and the mean and standard error plotted. The figure illustrates that reactive phosphate decreased from a relatively high "oceanic" value to a low "reef" value. At approximately 1000 meters, the reef water had nearly undetectable levels of reactive phosphate. Total phosphate also appeared to decrease to the 1000 meter area, but then increased (Figure 13).

To calculate the net uptake rate of phosphate by this community (gross exchange rate was determined to be proportional to the reactive phosphate concentration), the slopes of the reactive phosphate and the total phosphate were calculated using all data (Figure 13). There was no significant difference between the reactive and total phosphate slopes, as there was no significant difference between the ocean, reef differences (Table 5); therefore, it is now reasoned that the decrease in total phosphate was due to the net uptake of reactive phosphate. Since there is more error in the analysis of total phosphate, the decrease of reactive phosphate was used to calculate the net uptake of phosphate by the reef. This calculation results in a decrease of 0.082 mmoles P m^{-3} per 1000 meters of reef. The average advective flux over the reef flat was 0.06 $m^3 s^{-1} m^{-1}$ of reef front. The phosphate uptake rate was therefore 0.414 mmoles P $m^{-2} day^{-1}$ ((0.08 mmoles P m^{-3}) x (0.06 m^3 s^{-1}) x (s day $^{-1}$) x 1/1000m^2).

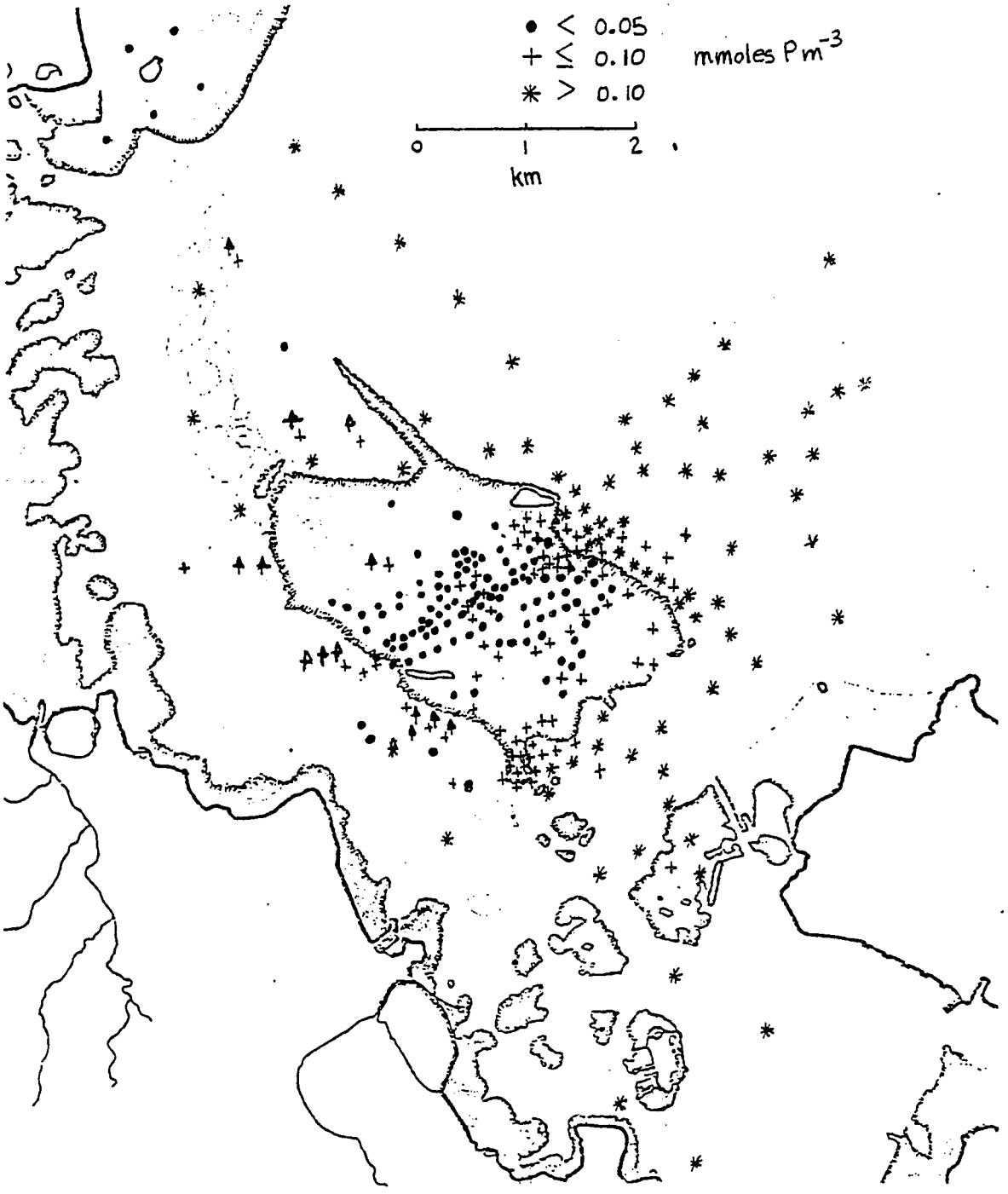

Figure 11: Reactive phosphate concentrations over the Kaneohe Bay barrier reef.

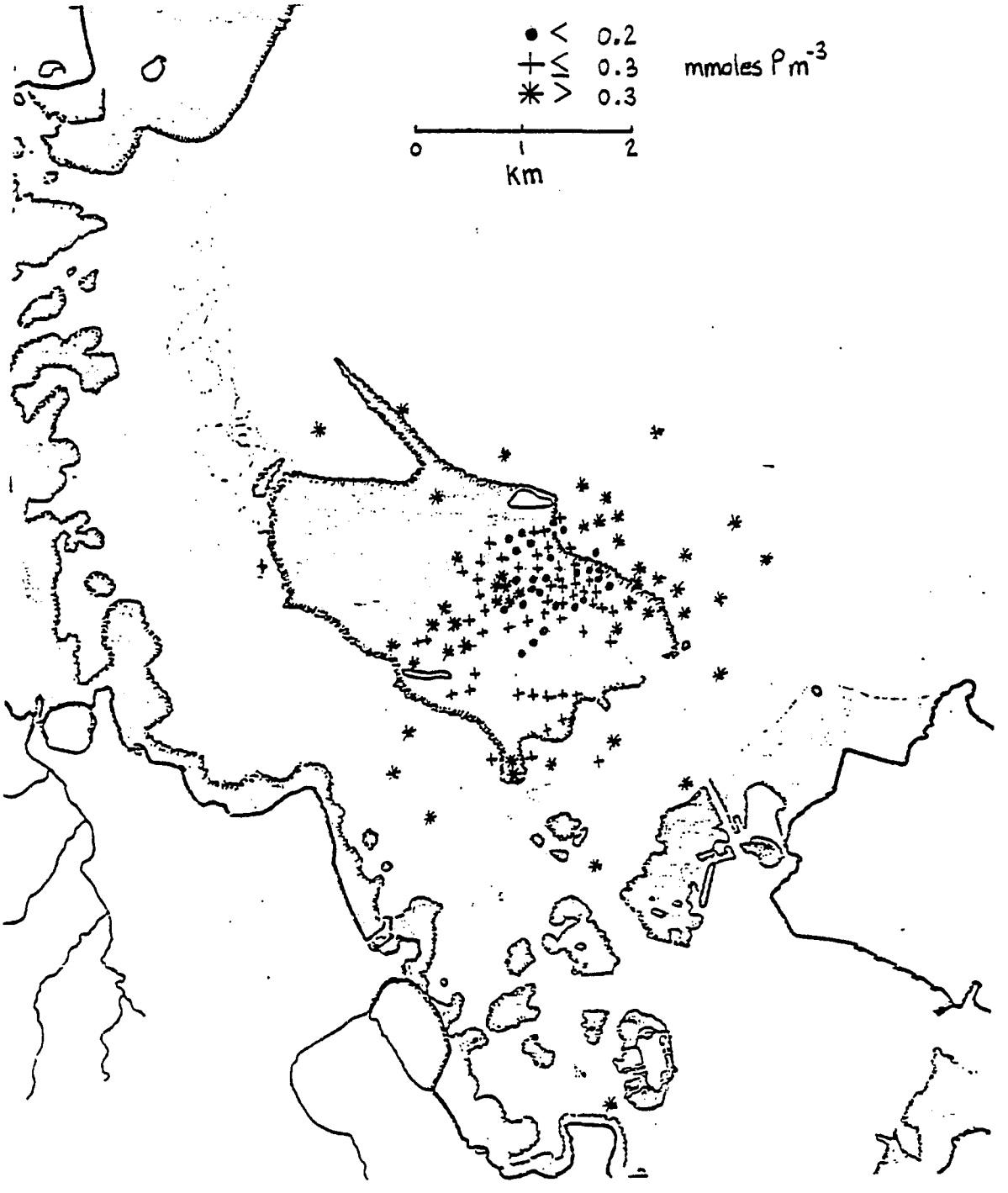

Figure 12: Total phosphate concentrations over the Kaneohe Bay barrier reef.

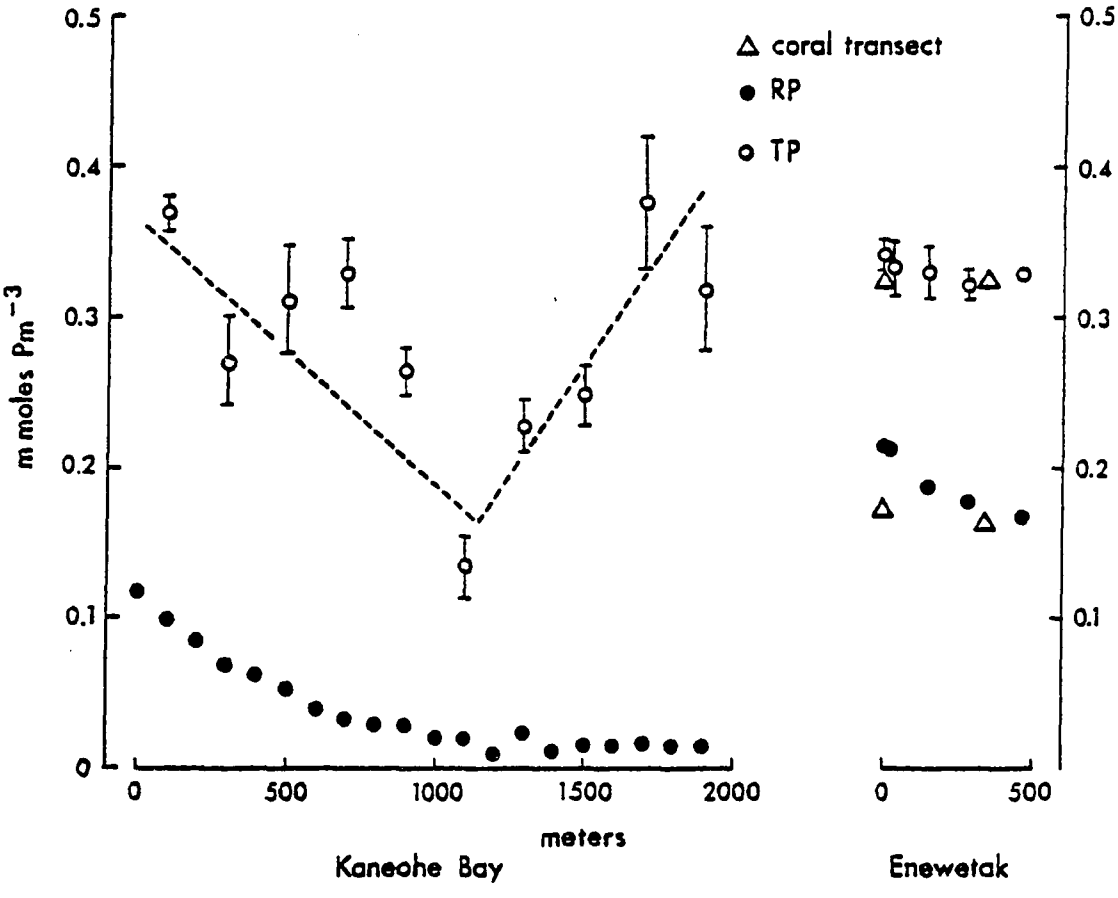

Figure 13: Phosphate concentration over three reef flat transects: Kaneohe Bay barrier reef, Oahu Hawaii, and two transects at Enewetak Atoll, Marshall Islands; algal and coral-algal. The solid dots are reactive phosphate means for all data collected throughout the sampling periods; the standard error of the mean is within the size of the dot. The open dots are total phosphate means for all data; the standard error of the mean is the height of the vertical bar. The mean values for Kaneohe Bay represent sampling throughout a year (see Table 5 for a breakdown). The means for Enewetak represent sampling throughout a month period (Pilson and Betzer 1973).

E. Producer C:P Ratios

To measure net productivity using phosphate, phosphate must be scaled to carbon. Both Pilson and Betzer (1973) and Smith and Jokiel (1977) for other reefs assumed the Redfield ratio (C:N:P = 106:16:1). However, samples of the primary producers from Enewetak and Kaneohe Bay were analyzed for carbon, nitrogen, and phosphorus, and the average C:P ratios of these algae were not even close to Redfield (see Appendix B for methods, additional results, and discussion).

Results:

The mean C:P ratios of Kaneohe Bay producers was used to scale phosphate to carbon. Multiplying this C:P scaling ratio (640:1) by the net phosphate uptake value for Kaneohe Bay (0.414 mmoles P $m^{-2}day^{-1}$) gave a net community production of 270 mmoles C $m^{-2}day^{-1}$.

IV. DISCUSSION

The conclusions of the previous experiments and field observations are: (1) Phosphate uptake rate as a percentage of the community respiration rate is proportional to the phosphate concentration. At typical concentrations of reactive phosphate over coral reefs (0.15 uM), the uptake of reactive phosphate is about 0.1% of the respiration rate (mole P uptake/mole O_2 respired). (2) The reef community can take up both orthophosphate and mono-ester bonded phosphate. The uptake rate of phosphate is limited by available phosphate concentration. (3) Phosphate adsorption is negligible compared to net processes of biological exchange, and (4) There is net uptake of phosphate by the Kaneohe Bay barrier reef flat (a reef flat with high residence time); that net uptake, scaled to carbon by the appropriate ratio of the C:P reef producers (640:1) is approximately 270 mmoles C $m^{-2}day^{-1}$.

Webb (1977) reported a gross primary production of 1170 mmoles C $m^{-2}day^{-1}$ and a net community production of 280 mmoles C $m^{-2}day^{-1}$ for the Kaneohe Bay barrier reef flat. The 24 hour respiration rate therefore (assuming the respiratory coefficient, CO_2 flux/O_2 flux, is approximately 1) is about 900 mmoles O_2 $m^{-2}day^{-1}$. A similar number, 850 mmoles O_2 $m^{-2}day^{-1}$, was reported for data collected by the coral reef chemistry class (Appendix A).

The results of the phosphate uptake experiments indicated that the uptake rate of phosphate was proportional to the reactive phosphate concentration. Assuming the relationship between reactive phosphate and uptake rate determined in the laboratory experiments is valid for in situ community respiration rates, reef communities can exchange phosphate with

the water column at rates from 0.04% to 0.2% of the community respiration, 0.05 uM to 0.3 uM reactive phosphate respectively. If 900 mmoles $O_2 m^{-2} day^{-1}$ is assumed as the community respiration rate of Kaneohe Bay barrier reef, then the phosphate uptake rate ranges between 0.8 mmoles P $m^{-2} day^{-1}$ on the fore-reef (0.12 uM reactive phosphate) to 0.4 mmoles P $m^{-2} day^{-1}$ (.05 uM reactive phosphate) near the middle of the reef. In the back regions of the reef where the phosphate concentration is virtually undetectable, the uptake rate is near zero. It was independently calculated from the reactive phosphate depletion over the reef flat that the net uptake of reactive phosphate by the reef community was 0.4 mmoles P $m^{-2} day^{-1}$. The net uptake of phosphate by this reef is therefore less than the gross exchange rate of phosphate by the reef.

The lagoon side of the Kaneohe barrier reef is a seagrass and rubble community. Results from one day of oxygen and carbon dioxide measurements indicate a net community respiration (Appendix A). It is noteworthy that the reactive phosphate remained extremely low across this section of the transect, yet the total phosphate appeared to increase (1000m - 2000m, Figure 13). High levels of reactive phosphate were found in the organic rich sediments of this area (Appendix A). I suggest that the net respiration of the community creates a significant loss of phosphate from the system. This loss appears as an increase of unavailable dissolved organic compounds, hence the increase in total phosphate. Reactive phosphate, since it is extremely low in these waters, is still required by the community for gross primary production. However other seagrass beds appear to export reactive phosphate (Kirkman et. al., 1979). It was suggested by Kirkman et. al. that the net release of reactive phosphate was through bacterial remineralization of detrital material collected in the marsh. Clearly this mechanism denotes a system with net respiration.

It was also noted in Kaneohe Bay that some coral rubble communities showed increases in nutrients (particularly ammonia, total phosphate, and total nitrogen) in the water over them while nearby areas were low in these nutrients. Low tide sampling of gelbstoff (water colored yellow) at Enewetak Atoll showed significantly higher nutrients (total phosphate, total nitrogen, ammonia, and even dissolved carbon) than high tide sampling. Extreme patchiness in oxygen concentration was also observed over the Kaneohe Bay barrier reef suggesting metabolic patchiness in the reef community (Appendix A). Sampling schemes must recognize some of these problems, or make use of them. Different communities within a whole reef ecosystem will show differences in metabolic processes.

The data of Pilson and Betzer (1973) from Enewetak were used to determine whether for this system the change in phosphate over the reef flats could be used to measure net productivity of the community. Unlike the Kaneohe Bay barrier reef flat, the residence time of water over the reef is only 10-30 minutes (see Introduction). Pilson and Betzer's (1973) data indicate that there is a significant decrease in reactive phosphate over an algal dominated reef flat but not a significant decrease in total phosphate (Figure 13). Like the Kaneohe Bay system, the rate of decrease of reactive phosphate over the reef is not significantly different from the rate of decrease of total phosphate. Therefore reactive phosphate, analytically, is more sensitive to the decrease in phosphate than total phosphate. The mean net uptake rate of reactive phosphate, as reported by Pilson and Betzer (1973), was scaled to carbon by the mean C:P ratio in the producers from Enewetak (500:1, Atkinson and Smith, Appendix B). The resulting net community productivities for two reef transects at Enewetak are similar to the net community productivities as determined by oxygen

and carbon dioxide. A summary of the net productivity calculations for Enewetak and Kaneohe Bay is presented in Table 6 (from Atkinson and Smith).

At Enewetak Atoll the concentration of reactive phosphate is higher than at Kaneohe Bay barrier reef (see Figure 13). Again, assuming the relationship determined in the laboratory experiments between reactive phosphate and phosphate uptake rate is valid for in situ community respiration rates, the reef communities at Enewetak take up phosphate at approximately 0.13% of the community respiration rate. Assuming the respiration rate is 500 mmoles O_2 $m^{-2}day^{-1}$ (see Table 6) the phosphate uptake rate is 0.65 mmoles P $m^{-2}day^{-1}$, or 319 mmoles C $m^{-2}day^{-1}$. This number is lower than the net productivity of 470 mmoles C $m^{-2}day^{-1}$ as determined from the removal of reactive phosphate from the water passing over the reef. I suggest that the experimental uptake rates determined in the laboratory are only rough estimates. Since most reefs reside in water near 0.1 to 0.2 uM reactive phosphate concentration, the uptake rate of phosphate by these communities will roughly be 0.1% of their respiration rate. I believe the higher concentration of reactive phosphate at Enewetak than at Kaneohe Bay establishes a higher phosphate uptake rate by the primary producers. This higher uptake rate therefore lowers the producer C:P ratio (640 for Kaneohe Bay and 490 for Enewetak, although these means are not significantly different) and increases the specific growth rate of these organisms. If the above interpretation is correct, the specific growth rates of primary producers are limited by phosphate. However, since there is a large amount of phosphate flowing over most coral reef ecosystems, the biomass of the system is <u>not</u> limited by phosphate (see later discussion).

Table 6. -- Comparison of coral reef organic carbon production estimated by CO_2 and O_2 flux measurements with production estimated by net P flux measurements.

Reef Flats	Production (mmoles C $m^{-2} day^{-1}$) (O_2 and CO_2) Gross	(O_2 and CO_2) Net	(P) Net
Kaneohe Bay, Hawaii			
algal transect	1170[a]	280[a]	270[b]
Enewetak Atoll			
algal transect	970[c]	470[c]	470[d]
coral-algal transect	500[c]	0[c]	0[d]

Footnotes:

(a) Webb (1977)

(b) C:P ratio = 640 for Hawaii

(c) Smith and Marsh (1973)

(d) Pilson and Betzer (1973)
C:P ratio = 490 for Enewetak

Pilson and Betzer (1973) did not use their data to calculate the net productivity of the system (see Introduction). Instead they showed that the change in reactive phosphate, or the net uptake of phosphate, did not match the instantaneous change in oxygen over a diurnal period. They even point out that there is not enough phosphate coming over the reef during low tide at mid-day to support gross primary production. Apparently, Pilson and Betzer erred in their analysis by assuming that the uptake of phosphate should be directly related to the instantaneous flux of oxygen (from photosynthesis), and by assuming Redfield ratios.

Smith and Jokiel (1976) realized that over a long period of time, weeks to months, the net depletion of phosphate in the water of Canton Atoll lagoon should be related to the net production of carbon in the system. However, they assumed that carbon and phosphorus should be matched according to the Redfield ratio. Smith and Jokiel (1976) had to invoke a net carbon dioxide evasion from the lagoon water to the atmosphere to get rid of the excess carbon in the budget. This carbon dioxide evasion was against a P_{CO_2} gradient from the atmosphere to the water. Smith and Jokiel recognized however that if no net evasion of carbon dioxide from the lagoon to the air were to occur, the excess carbon must be incorporated into organic material with a C:P ratio of 500:1. They dismissed this alternative interpretation because it suggested extreme nutrient limitation of the producers (based on comparisons with the Redfield ratio).

Changes in reactive phosphate can be used to measure net community production of reef ecosystems. The measured changes in phosphate must be scaled to carbon by the appropriate C:P ratio in the producers. The reef community apparently takes up phosphate at a continual rate, night and

day, as long as the net uptake matches the net production on a daily or weekly basis. Uptake rates of phosphate determined from short-term incubations of water are therefore good approximations of daily and weekly production. I will now use two other ^{32}P labeling studies to present the topic of phosphate recycling in coral reefs.

The first study is a "closed" tracer experiment in large volume aquaria and in a pond. The aquaria were replete with both planktonic and benthic organisms (Whittaker, 1961). ^{32}P was introduced into the aquaria and the organisms sampled throughout a two month period. ^{32}P was removed from the water rapidly and found first in plankton, attached plants, and organic surface films. As time progressed, the ^{32}P moved slowly up the food chain and by a month later was found in the higher trophic levels. There was a net accumulation in the sediments. Throughout the experiment, ^{32}P was found in the water. Whittaker concluded that the plankton, algae, and microorganisms exchanged (uptake and release) ^{32}P with the water. Whittaker also pointed out that the rapid adsorption of ^{32}P on most surfaces was probably biologically related and important to the community absorption of phosphorus. There was little uptake of ^{32}P in an aquarium poisoned with formaldehyde. Other workers have shown that plankton, algae, and microbial communities exchange phosphate readily with the water (Odum, 1958; Johannes, 1965; and Lean and Nalewajko, 1976). The water therefore is the primary source and sink for biologically mediated phosphate recycling.

The next experiment is a little different. Large amounts of ^{32}P were dumped into a stream, and the stream water and biota were sampled at several locations for twelve miles downstream and throughout the following year (Ball and Hooper, 1961). The experiment was repeated. The

^{32}P was removed from the flowing stream rather quickly, the "½-distance" being approximately a kilometer. It was rapidly taken up by the periphyton (algal communities living on rock surfaces). As expected, ^{32}P moved into the higher trophic levels of the stream (snails, crustacea, etc) and even into the soils and plants near the stream bank. The interesting aspect of this experiment however is that the pulse of ^{32}P moved down the stream in the periphyton. The investigators concluded that the periphyton biomass was vital to the uptake, release, and retention time of the ^{32}P. ^{32}P was released into the flowing water and taken up again by downstream communities. They estimated a 20 day retention time by the periphyton. This experiment demonstrates that phosphate is exchanged by these benthic plants in a flowing water environment. The epiphytic plant community in the stream relies on exchange with the water, as do the communities in the aquaria.

The exchange of phosphate reported in this dissertation suggests that reef communities depend heavily on the advecting water for their source of phosphate. Pomeroy et. al. (1974) labeled subcommunities of reef organisms with ^{32}P, describing uptake and release of phosphate. They suggested that reef producers fall into two catagories, those that exchange phosphate with the water column continually and those that "recycle" phosphate internally. Primary producers clearly vary in their retention times of phosphate, but both cycle phosphate relatively easily into the surrounding water.

Coral reef communities are probably not tightly recycling phosphorus. The following model will illustrate this concept. The reef flat ecosystem may be partitioned into several phosphorus pools. They are: (1) phosphate in the water column, excluding reef organisms; (2) phosphate in reef

producers; (3) phosphate in reef consumers; and (4) phosphate in the calcium carbonate substrate. The size and turnover rates of these pools are summarized in Table 7. The water column pools are extremely small but have a high turnover rate, while the benthic pools are large and have a slow turnover rate. The amount of phosphorus necessary to support daily gross production per day is small compared to the average amount of phosphorus advecting over the reef. The reef producers take up phosphate uniformly through the day, integrating their nutritional requirement over several days. The exchange of phosphate between the water and the benthos creates an open cycling with the water column. Phosphate is therefore continually being "recycled" through the water overlying the reef. The amount of phosphate recycled through the water column as opposed to the total amount of phosphate available to the reef producers can be expressed as the ratio of the amount excreted or released to the water to the total amount available (advective amount plus released amount) on a daily basis. This ratio expressed as a percentage indicates that the amount of phosphate released into the water column at Enewetak is only about 5% of the total available phosphate. Since the excreted pool is well mixed with the reactive phosphate in the water, no more than 5% of the released phosphate can be recycled in this system. In systems where advection of phosphate is low, the amount of phosphate that is recycled becomes large. A similar calculation for Kaneohe Bay shows that the amount of phosphate releasd by the community is approximately 80% of the total amount of phosphate available. Gross primary production of this reef can be maintained by recycled phosphate but net community production is still maintained by the advection of phosphate over the reef. In enclosed

Table 7. -- Pool size, renewal rate, and turnover times for Enewetak reef flat phosphorus pools. Turnover time = pool size/renewal rate. Numbers labeled with "*" were calculated from the other two parameters by the above equation.

Average pool sizes for water column pools are based on standing water column of 0.556 m (actual mean tidal range at Enewetak is 0.82 m) and transect length of 455 m. Plankton concentration over reef flat is from Odum and Odum (1955), reactive phosphate and total phosphorus concentrations are from Pilson and Betzer (1973).

Renewal rates for water column phosphate pools are based on volume transport of 0.556 m^3 sec^{-1} m^{-1} reef front (Atkinson et al, 1981). Plankton concentration of oceanic water is from Odum and Odum (1955), reactive phosphate and total phosphorus are from Pilson and Betzer (1973).

Pool sizes for producers, herbivores, and carnivores were calculated from dry weight biomass estimates (Odum and Odum 1955), assuming consumers are 1% phosphorus by weight (Pomeroy and Kuenzler 1969), and producers are .1% by weight.

$CaCO_3$ pool size estimated assuming available substrate is 0.01 m deep, 2.7 g/cc, 50% porosity, and 0.01% phosphorus by weight.

Renewal rate for producers was calculated from gross primary production (0.5 moles C m^{-2} day^{-1}), assuming all carbon is fixed to biomass of C:P=500. Renewal rates for herbivores and carnivores were determined by excretion of total phosphorus (Pomeroy and Kuenzler 1969) and calculated from estimates of turnover time, marked by "*" (Pomeroy and Kuenzler 1969). The community turnover time was calculated by a weighted average of turnover times for different groups of animals. Biomass of different groups of animals are from Odum and Odum (1955) and turnover rates (based on individual organism excretion rates) are from Pomeroy and Kuenzler (1969).

Pools	Pool Size mmoles P m^{-2}	Renewal Rate mmoles P m^{-2} day^{-1}	Turnover Time size/rate days
WATER COLUMN			
net plankton	0.01	0.4	0.023*
reactive phosphate	0.09	18	0.005*
total phosphate	0.30	34	0.009*
BOTTOM POOLS			
producers	23	1	23
consumers	46	0.30 (.15*)	307 (153)
$CaCO_3$ substrate	44	unknown	geological time

basins such as Canton Lagoon, on the average the amount of recycling in the water column will be large.

Coral reef ecosystems do not necessarily recycle their phosphorus tightly. Apparently, reef communities have an open cycling of phosphate through the water column.

V. CONCLUSIONS

1. The exchange rate of phosphate between the reef benthic community and the water column depends on the phosphate concentration of the water. For reefs residing in 0.15 uM P water it is approximately 0.1% of community respiration (mole P/mole O_2 respired). Phosphate exchange includes both inorganic phosphate and organic phosphate. The inorganic adsorption and desorption reactions with the reef benthos appear to be small compared to the uptake and release rates by the community.
2. If reef flats show a net change of phosphate, then this net change can be used to measure community biomass gain (or loss) if phosphorus is scaled to carbon by a C:P ratio of approximately 500-650:1.
3. The advection of phosphate over a typical reef is large compared to the phosphate requirements of the reef. This large advection of phosphate can support a large benthic biomass, but the low concentration of nutrients probably affects the specific growth rate of the reef producers.
4. Phosphate recycling between coral reef organisms is not tight, nor is it strictly controlled by biological factors as generally believed by earlier investigators.

VI. IMPLICATIONS

Since phosphate is openly cycled through the water column and advection of phosphate is usually large, the producer biomass can accrete until space (substratum) becomes the limiting factor. Competition among reef producers is therefore probably space-related. Many strategies for living on the reef will evolve; however all producer strategies will attempt to avoid washout from the system and to withstand physical damage by water motion. Hence this kind of competition among producers establishes a system with both slowly growing, calcifying producers and relatively fast growing burrowing forms of filamentous algae and well-attached thalloid algae. Rapid growth and reproduction of producers are not essential for success in this kind of an ecosystem. Slow growth with the resistance to predation can be as successful as rapid growth, reproduction, and recolonization.

In this ecosystem of advecting nutrients with open cycling of the nutrients in the water, grazing activity on the producers does not necessarily regulate the nutrient concentration. The nutrient regime is heavily influenced by the advection of water. Hence, the turnover of limiting nutrients is not controlled by grazing pressure. If the nutrient regime is not regulated by grazing, then production and specific growth rate of the producers (productivity per biomass) is not controlled by higher trophic levels. The food chain probably does not necessarily orient itself to optimize the passage of carbon, nitrogen, or phosphorus to higher trophic levels, as has been suggested for pelagic ecosystems. Biomass and turnover of higher trophic level consumers might be limited by habitat and higher trophic level competition, not by available plant material.

If increased phosphate concentration increases phosphate uptake rate and specific growth rate of the producers, then coral reefs located in high phosphate concentration water might experience severe space competition between the slow growing calcifying producers and the more rapid growing algae.

APPENDIX A

Ocean 770, Fall 1980: Coral Reef Chemistry: Kaneohe Bay Barrier Reef Expedition. Chave, K. E.; S. V. Smith; C. Agegian; M. Atkinson; D. Burns; E. H. Chave; S. Crowell; K. Grome; J. Morrissey; and C. Rice.

On October 4 and 5, 1980 the Oceanography 770 class conducted a 24-hour reef metabolism expedition on the Kaneohe Bay barrier reef. The purpose of the expedition was to give the students an opportunity to learn chemical measurement techniques and to interpret field data. This summary is from the contributed papers of the class. The data are available from K. E. Chave, University of Hawaii Oceanography Dept., or any other participant.

Methods:

The sampling of the reef environment involved water and benthic sampling at two stationary sites, one in the turf zone and one in the seagrass zone (see Figure 1 of this dissertation); and water sampling of the whole reef from the ocean to the lagoon by drifting over the reef flat. The following variables were measured: water depth, current speed, salinity, water temperature, solar radiation, wind speed, dissolved oxygen, total carbon dioxide, alkalinity, nitrate, ammonia, reactive phosphate, particulate organic and inorganic carbon, particulate nitrogen, particulate phosphate, detrital load, and benthic biomass.

Water depth was measured with a calibrated line, current speed estimated with dye and plastic, gallon bottle drogues. Salinity was measured with a Plessey conductivity salinometer, oxygen and temperature with a YSI 57 oxygen meter. Total carbon dioxide and alkalinity were determined

by the technique of Smith and Marsh (1973), and the nutrients were analyzed with a Technicon II Autoanalyzer. Nutrient water samples were collected with a 50 ml syringe, the water immediately filtered through a 0.45 um GFC glass fiber filter and then either frozen or analyzed within several hours on the autoanalyzer. Two liters of water were collected in plastic bottles and filtered onto pre-combusted 0.45 um GFC glass fiber filters in the laboratory for CHN and P particulate analysis. Detrital load was estimated by collecting detritus in stationary nets.

Results:

The weather was beautiful, sunny days with little wind. The current meandered over the reef from ocean to lagoon at speeds of 0-3 cm s^{-1}. Salinity increased over the reef flat both during the day and the night. The water temperature was higher over the reef than ocean or lagoon during the day but lower at night. Oxygen increased over the reef during the day but decreased at night; and the opposite was true for total carbon dioxide. Alkalinity, phosphate and nitrate showed a significant decrease over the reef flat, while ammonia and particulates were variable.

Data collected from the single locations, the turf and seagrass zones, showed that there were diurnal trends in oxygen and total carbon dioxide, but not in the nutrient parameters. The daily variations in oxygen and carbon dioxide were used to calculate the gross productivity and net productivity of the system. These calculations indicated that the turf zone had a gross productivity of about 850 mmoles C $m^{-2}day^{-1}$ (2% of solar energy) and a net productivity of nearly 0: and the turf zone had a gross production of 200 mmoles C $m^{-2}day^{-1}$ and a net consumption of 200. The biomass of the turf area was estimated to be 900 g m^{-2} (wet wt.) while the seagrass area was estimated to be half that, 490 g m^{-2} (wet wt.).

The detrital load was estimated to be sufficient for excess heterotrophy of the seagrass region. The sediments of the seagrass area were reported to be rich in organics, hydrogen sulfide, and nutrients. The net productivity of the turf region was low, however, oxygen transects of the reef flat suggested that the macroalgal zone, immediately behind the turf zone, had a higher productivity than the turf zone. It was suggested that this zone produced the excess material required for net respiration by the seagrass bed.

Calcification was shown to be equivalent to a yearly rate of 10 kg Ca CO_3 $m^{-2}yr^{-1}$ in the turf zone and a dissolution rate of equal magnitude in the seagrass zone.

The particulate load and the ratio of C, N, and P in the particulates appeared to be a function of the surf activity and tide height. It was reasoned that inorganic resuspension influenced the nature of the particulate material.

It was concluded from this work that the Kaneohe Bay barrier reef shows typical reef metabolism and zonation. The fore-reef communities are net producers, while the back-reef communities (rubble and seagrass) are net consumers.

APPENDIX B

The following paper has been submitted for publication: "Carbon:Nutrient Ratios of Benthic Marine Plants," by M. Atkinson and S. V. Smith of the Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822 and also of Hawaii Institute of Marine Biology, P. O. Box 1346, Kaneohe, Hawaii 96744.

ABSTRACT

The average C:N:P ratio of seagrasses and marine algae is approximately 700:35:1. In comparison with plankton, benthic plants are greatly depleted in N and P relative to C. The amount of nutrients required to support a particular level of net productivity, biomass, and net accumulation of organic matter is therefore much lower for benthic plants than it is for plankton.

A useful unifying concept in biological oceanography is expressed as the so-called "Redfield Ratio." As widely discussed (e.g., 1), the carbon:nitrogen:phosphorus (C:N:P) atomic ratio of organisms in the sea is ordinarily near 106:16:1. The ratio is based on extensive analyses of marine plankton. A corollary to this standard compositional ratio of marine organisms is the observation that the net uptake and release of nutrients through biochemical processes in the sea also tend towards this same ratio. Indeed, the inorganic N:P ratio of deep-ocean water is approximately 16:1, apparently as a result of the decomposition of organic materials to an inorganic nutrient end product. The inorganic C content of deep-ocean water does not fit the Redfield Ratio, because inorganic C is far more abundant in seawater (relative to the Redfield Ratio) than is either N or P.

Deviations from the Redfield Ratio in phytoplankton are often used to infer the nutrient limiting growth. Phytoplankton deprived of P during growth have N:P ratios greater than 30:1, while phytoplankton deprived of N during growth have N:P ratios less than 10:1. C:N and C:P ratios are also dependent upon the growth conditions. Goldman et. al. (2) have reasoned that phytoplankton with a composition near the Redfield Ratio are growing at their maximal growth rates.

The Redfield Ratio is often extended to aquatic systems other than phytoplankton-based ones. Odum (3) gives the ratio general ecological significance by using it as an example of the relationship between C, N, and P during production. He explains how measuring different variables (O, C, N, P) can be used to determine the different types of production. It is not clear that ecologists applying the Redfield Ratio to ecosystems other than planktonic ones pay sufficient heed to its limitations. We

document here that seagrasses and benthic algae deviate markedly in their carbon:nutrient composition from the Redfield Ratio, and we suggest that this discrepancy is ecologically significant.

The data presented here include some information we have collected from the open literature along with more extensive analyses performed in our own laboratory. Relevant literature data are surprisingly limited. The availability of CHN analyzers makes C:N ratios easily obtainable, hence relatively available in the literature. Fenchel and Jørgensen (4) state that the C:N ratios of seagrasses and algae range from 10:1 to 70:1; all of this range lies well above the Redfield C:N ratio of 6.6:1. Much less information, however, is available for P. Fenchel and Jørgensen (4) report a C:P ratio of about 200:1 for macrophytes (about twice the Redfield C:P ratio of 106:1). However, no actual data are given in their review, nor can C:N:P ratios for individual organisms be readily extracted from the references they cite.

Published data sets including both N and P in organic material tend not to include C. Some such data sets do include other elements present in the organic material (especially S, K, Mg, Ca, Na, and Cl). For two such data sets, we estimated weight per cent C to be percent C in carbohydrate (40%), minus the summed weight per cent of other ions. For both algae (5) and seagrasses (6) average C estimated by this procedure was 27% of the dry weight. This average is close to the average %C we have directly measured (Table 1). Within the C, N, and P percentages in organic materials, the C:N:P ratio is more sensitive to N and P than to C. We have therefore used this average C value in the absence of direct C data, and we have restricted our use of published data to tabulations containing at least N and P.

Table 1. Weight percent C and atomic C:N:P ratios in marine macrophytes

Taxon	Plant Part	Phylum (1)	Locality	%C (2)	C:N:P (3)	Ref. (4)
Acanthophora spicifera		R	Hawaii	22	555:38:1	
" "		R	N. Queensland	26	1093:62:1	
Alaria crassifolia		P	Japan	*	143:16:1	(5)
Amphibolis griffithii	leaves	S	W. Australia	30	535:20:1	
" "	stems	S	W. Australia	30	982:27:1	
Amphiroa foliacea		R	N. Queensland	4	295:16:1	
Asparagopsis sp.		R	Enewetak	11	495:47:1	
Boodlea sp.		Ch	Enewetak	19	605:71:1	
" "		Ch	Enewetak	10	371:33:1	
Calothrix sp.		Cy	Enewetak	16	466:46:1	
" "		Cy	Enewetak	16	429:52:1	
Cladophora sp.		Ch	Enewetak	17	265:38:1	
Cladostephus spongiosus		R	Corsica	29	1927:70:1	
Codium sp.		Ch	Rhode Island	20	251:31:1	
C. arabicum		Ch	Hawaii	19	468:24:1	
C. bursa		Ch	Corsica	15	971:74:1	
Colpomenia sinuosa		P	N. Queensland	15	437:18:1	
Cymodocea nodosa	leaves	S	Corsica	37	408:15:1	
C. serrulata	leaves	S	N. Queensland	38	638:18:1	
" "	leaves	S	N. Queensland	*	410:19:1	(6)
" "	rhizomes	S	N. Queensland	*	872:13:1	(6)
Cystoseira balearica		P	Corsica	31	995:54:1	
C. fimbriata		P	Corsica	27	1896:68:1	
C. spinosa		P	Corsica	27	589:61:1	
C. stricta		P	Corsica	31	1124:65:1	
C. trinodis		P	N. Queensland	31	933:35:1	
Dictyosphaeria cavernosa		Ch	Hawaii	14	623:31:1	
D. versluysii		Ch	N. Queensland	17	478:20:1	
Dictyota acutiloba		P	Hawaii	36	744:35:1	
D. pardalis		P	N. Queensland	37	1201:58:1	
D. sandvicensis		P	Hawaii	36	951:53:1	
Ecklonia radiata		P	W. Australia	34	364:14:1	
Enhalus acoroides	leaves	S	N. Queensland	*	317:16:1	(6)
" "	rhizomes	S	N. Queensland	*	410:5:1	(6)
" "	leaves	S	N. Queensland	36	444:18:1	
" "	leaves	S	Palau	39	1000:48:1	
" "	rhizones	S	Palau	35	695:16:1	
Enteromorpha flexuosa		Ch	N. Queensland	7	362:16:1	
Galaxaura rugosa		R	Hawaii	13	545:31:1	
Gracilaria sp.		R	Hawaii	20	315:16:1	
Gracilaria verrucosa		R	Japan	*	291:43:1	(5)
G. sp.		R	Virginia	37	819:29:1	
Halimeda sp.		Ch	Enewetak	14	872:42:1	
H. discoidea		Ch	Hawaii	22	499:47:1	
H. opuntia		Ch	N. Queensland	6	488:33:1	
H. tuna		Ch	Corsica	14	501:67:1	

Table 1 (continued)

Taxon	Plant Part	Phylum (1)	Locality	ZC(2)	C:N:P(3)	Ref.(4)
Halodule univervis	leaves	S	N. Queensland	*	465:13:1	(6)
" "	rhizomes	S	N. Queensland	*	388:14:1	(6)
" "	leaves	S	N. Queensland	36	623:18:1	
Halophilia decipiens		S	N. Queensland	*	268:11:1	(6)
H. hawaiiana		S	Hawaii	24	447:18:1	
H. ovalis		S	W. Australia	16	388:13:1	
" "		S	N. Queensland	*	465:9:1	(6)
H. ovata		S	N. Queensland	*	698:9:1	(6)
H. spinulosa		S	N. Queensland	*	465:10:1	(6)
" "		S	N. Queensland	29	256:11:1	
Heterochordia abietina		P	Japan	*	139:17:1	(5)
Hydroclathrus clathratus		P	Hawaii	25	400:20:1	
" "		P	N. Queensland	18	300:18:1	
Hypnea valentiae		R	N. Queensland	20	612:31:1	
Iridaea cordata		R	California	29	388:22:1	
Kjellmaniella crassifolia		P	Japan	*	239:13:1	(5)
Laminaria angustata		P	Japan	*	279:12:1	(5)
L. japonica		P	Japan	*	183:9:1	(5)
L. religiosa		P	Japan	*	384:25:1	(5)
L. dentigera	stipe/blades	P	California	27	390:18:1	
Laurencia sp.		R	N. Queensland	26	1274:66:1	
L. sp.		R	Hawaii	25	571:62:1	
Lyngbya majuscula		Cy	Enewetak	21	302:38:1	
" "		Cy	Hawaii	43	377:40:1	
Macrocystis pyrifera	blades	P	California	29	222:11:1	
Monostroma latissimum		Ch	Japan	*	1316:58:1	(5)
Nereocystis luetkeana	blades	P	California	23	176:18:1	
Padina japonica		P	Hawaii	18	594:22:1	
P. tenuis		P	N. Queensland	24	584:24:1	
P. sp.		P	Hawaii	16	566:29:1	
" "		P	Corsica	14	1271:76:1	
Peyssonnelia sp.		R	Corsica	23	744:59:1	
Phyllospadix scouleri	leaves	S	California	36	509:24:1	
Porphyra yezoensis		R	Japan	*	137:23:1	(5)
Posidonia oceanica	leaves	S	Corsica	33	956:39:1	
" "	roots	S	Corsica	38	3550:61:1	
" "	rhizomes	S	Corsica	35	1749:40:1	
P. ostenfeldii	leaves	S	W. Australia	33	1070:29:1	
" "	roots/rhizomes	S	W. Australia	34	1297:24:1	
P. sinuosa	leaves	S	W. Australia	22	512:16:1	
" "	roots	S	W. Australia	21	809:18:1	
Polysiphonia sp.		Ch	Rhode Island	22	186:27:1	
Ruppia maritima	leaves	S	Virginia	27	457:29:1	

Table 1 (continued)

Taxon	Plant Part	Phylum (1)	Locality	%C(2)	C:N:P(3)	Ref.(4)
Sargassum sp.		P	Hawaii	28	1031:20:1	
" "		P	Hawaii	20	765:20:1	
" "		P	N. Queensland	30	1106:38:1	
" "		P	N. Queensland	43	687:38:1	
" "		P	N. Queensland	32	770:31:1	
" "		P	W. Australia	38	537:22:1	
Schizothrix sp.		Cy	Enewetak	15	554:21:1	
" "		Cy	Enewetak	16	501:33:1	
" "		Cy	Hawaii	15	398:33:1	
Sphaerococcus coronopifolius		R	Corsica	36	1625:182:1	
Spyridia sp.		R	Virginia	19	240:31:1	
Stypopodium sp.		P	Hawaii	26	847:35:1	
Syringodium isoetifolium	leaves	S	N. Queensland	*	332:13:1	(6)
" "	rhizomes	S	N. Queensland	*	775:10:1	(6)
Thalassia hemprichii	leaves	S	N. Queensland	31	599:27:1	
T. testudinum	leaves	S	Barbados	*	445:32:1	(14)
" "	rhizomes	S	Barbados	*	601:20:1	(14)
Turbinaria ornata		P	Hawaii	28	1090:20:1	
" "		P	N. Queensland	35	925:22:1	
Udotea petiolata		Ch	Corsica	24	527:78:1	
Ulva sp.		Ch	Rhode Island	35	336:35:1	
U. reticulata		Ch	Hawaii	32	1051:80:1	
Undaria pinnatifida		P	Japan	*	307:18:1	(5)
Zostera capricorni	leaves	S	N. Queensland	*	349:17:1	(6)
" "	rhizomes	S	N. Queensland	*	465:8:1	(6)
" "	leaves	S	N. Queensland	32	302:9:1	
Z. marina	leaves	S	California	38	274:38:1	
" "	leaves	S	Rhode Island	31	481:27:1	
" "	leaves	S	Virginia	41	584:41:1	

Footnotes:

(1) S = Spermatophyta; P = Phaeophyta; R = Rhodophyta; Ch = Chlorophyta; Cy = Cyanophyta

(2) Not directly available except for our data

(3) Value of C figured at 27% for data sources other than our own

(4) Values from our laboratory unless noted otherwise

Our own samples were handled as follows. Algae were collected either by us or by a number of cooperators; epiphytes were removed; the algae rinsed quickly with fresh water, air dried, oven dried, and then ground to a powder. A Hewlett Packard 185B CHN analyzer was used to determine C and N, with the procedure of Hirota and Szyper (7) being used to correct for inorganic carbon. Phosphorus was determined by digesting pre-weighed, ground material in boiling 7 normal sulfuric acid. The solution was brought to a concentration of 5% potassium persulfate in water and boiled. Samples were then diluted with distilled water and analyzed for reactive phosphate with a Technicon II Autoanalyzer.

Table 1 contains the results of our own analyses and those obtained from the literature. While there is a great deal of variation in the C:N:P ratio of the benthic plants, the average ratio within phyla and the overall average clearly differ from the Redfield ratio. The average C:N:P ratio of a wide variety of macrophytes is approximately 700:35:1 (based solely on our analyses). The average C:N ratio is well within the range reported by Fenchel and Jørgensen (4), but the C:P ratio we obtain is above their estimate. There are no discernible differences among phyla, but there are differences among locations. Few individual analyses of these benthic plants approach the Redfield C:P ratio (106:1) although several samples overlap the Redfield C:N ratio (6.6:1) and the Redfield N:P ratio (16:1). Thus, in comparison with plankton C:N:P ratios, the benthic plants appear most deficient with respect to P and somewhat less deficient with respect to N.

At this point it is difficult to interpret the physiological significance of these results. The average C:N:P ratio we have found in benthic plants would suggest to those who study phytoplankton that these plants

have a low specific growth rate and are limited for P. Data from Gerloff and Krombholz (8) indicate 23 freshwater benthic plants in a highly fertile lake had a mean N:P ratio of 15:1, while the mean N:P ratio of 15 benthic plants in a relatively infertile lake was 30:1. The benthic plants we have examined might be nutrient limited, but as these plants were collected from a variety of ecosystems with different nutrient regimes, and as we have no direct data for nutrient limitation at the collection sites, we hesitate to make such a general statement for the data at hand.

Another interpretation of the high C:nutrient ratios and the high variability in the ratio is that the benthic plants have proportionately more carbon than do plankton in structural material; this might vary depending on the growth stage or season. Clearly, whole plants yield different results than the growing portion of the plants. This fact is brought out in analyses of several of the seagrasses, tabulated by major plant parts. Translocation of carbon has been reported for some kelp (9), and this process will affect carbon:nutrient ratios within the plant.

As stated by Odum (3), net community production of a benthic ecosystem can be estimated using the depletion of P and scaling it to C. It is important that the appropriate C:P ratio be applied to the scaling, rather than wholesale application of the Redifeld Ratio. Consider the following example. The net decrease in P was measured in water as it crossed two algal dominated coral reef flats; changes in P were scaled to C using the mean ratio measured in benthic primary producers from each of these sites. Table 2 presents the results. The net community production of biomass as estimated by this technique was compared with the net primary production

Table 2. Comparison of coral reef organic carbon production estimated by CO_2 and O_2 flux measurements with production estimated by net P flux measurements.

Reef Flats	Production (mmoles C $m^{-2}day^{-1}$) (O_2 and CO_2) Gross	(O_2 and CO_2) Net	(P) Net
Kaneohe Bay, Hawaii			
algal transect	1170(1)	280(1)	270(2)
Enewetak Atoll			
algal transect	970(3)	470(3)	470(4)
coral-algal transect	500(3)	0(3)	0(4)

Footnotes:

(1) Webb (10)

(2) Atkinson, present data, for P uptake; Table 1: C:P ratios = 640 for Hawaii

(3) Smith and Marsh (11)

(4) Pilson and Betzer (15) for P uptake; Table 1: C:P ratio = 490 for Enewetak

estimated from the difference between photosynthesis and respiration using changes in CO_2 and O_2 (10 and 11). In both examples, the two measures of community production compare well with one another.

Since the average C:nutrient ratio in seagrasses and benthic algae is about 3-5 times greater than the C:nutrient ratio in phytoplankton, the benthic plants require a lower nutrient supply than the phytoplankton to support an equivalent level of biomass and net productivity (based on carbon). Moreover the high C:nutrient ratios in benthic plants suggest that they are not nutritionally satisfactory food sources (4, 12). Hence, these plants may resist microbial decomposition and may form significant net accumulations of organic matter (13).

We conclude that benthic marine plants differ substantially in their C:nutrient ratio from the classical Redfield Ratio. The difference, in the direction of greatly depleted N and especially P relative to C, is of interest beyond idle curiosity. Notions of the role of marine biota in the cycling of essential elements may be affected by this large deviation of benthic plant composition from the Redfield Rtio.

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