CHEMICAL STOICHIOMETRY OF LAGOONAL METABOLISM

Preliminary Report on an Environmental Chemistry Survey of Christmas Island, Kiribati

Sponsored by

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Preliminary Report on an Environmental Chemistry Survey of Christmas Island, Kiribati

by

S.V. Smith, S. Chandra, L. Kwitko, R.C. Schneider,
J. Schoonmaker, J. Seeto, T. Tebano, and G.W. Tribble

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ABSTRACT

The mass balance of carbon, silicon, nitrogen, and phosphorus in the lagoon of Christmas Island has been calculated. There is no net silicon flux, consistent with the composition of coral reef systems. Dissolved organic nitrogen is released by the lagoonal system and exported. Carbon, phosphorus, and inorganic nitrogen are all slowly taken up by the system. The ratio of net inorganic N:P uptake matches the compositional ratio of incoming water and is very low in comparison with the compositional ratio of benthic plants.

The observed patterns of carbon, nitrogen, and phosphorus flux can be explained by a relatively simple model. Net metabolism of this system -- and that of other confined water bodies -- is limited by the availability of phosphorus. Just sufficient nitrogen is fixed to use the available phosphorus. Export of dissolved organic nitrogen simply removes a largely unutilized by-product of the nitrogen fixation.

ACKNOWLEDGMENTS

Besides the scientific information gained from this investigation, we have used the study as a training exercise. Although each of the co-authors of this report brought his/her own talents into the study, only the senior author has had previous extensive experience in environmental chemistry surveys of the kind reported here. This opportunity to conduct the study as a training exercise was made possible under the auspices of the International Sea Grant Program. We thank Dr. Philip Helfrich (University of Hawaii) and Dr. Uday Raj (University of the South Pacific) for providing us this opportunity. The work has also been complemented by a parallel survey at Fanning Atoll, funded through the National Science Foundation.

We particularly thank the following individuals of Christmas Island for their assistance in this study: Baraniko Raobati, Patrick Lawrence, Boitabu Smith, and John Bryden. Valuable information on the birds of Christmas Island was provided by Dr. Ralph Schreiber.

Joann Sinai and Ted Walsh have been instrumental in preparing us for this expedition and in subsequent rapid sample analysis upon our return. All logistical aspects of this study have been greatly aided by the ongoing efforts and good humor of Peter Rappa.

We thank Marlin Atkinson, Ed Laws, Steven Dollar, Phil Helfrich, and Fred Mackenzie for critical comments on this manuscript.

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INTRODUCTION

Ecosystems such as coral atolls can be viewed as diverse assemblages of plants and animals living in a complex and heterogeneous environment. It is quite natural to conclude from this view of complexity that such systems are not amenable to generalization. We hope that this report is written with a more optimistic outlook.

The water chemistry of coral reef environments can exert influence on the biological function of the system and can record that biological function. Simple principles of material mass balance, really no more than bookkeeping of the sources and fates of chemical components in the environment, are applied here as a basic description of the main lagoon of Christmas Island (or Kritimati), Republic of Kiribati (Figures 1 and 2); and observations for the Christmas Island lagoon have been compared with analogous observations for other similar ecosystems.

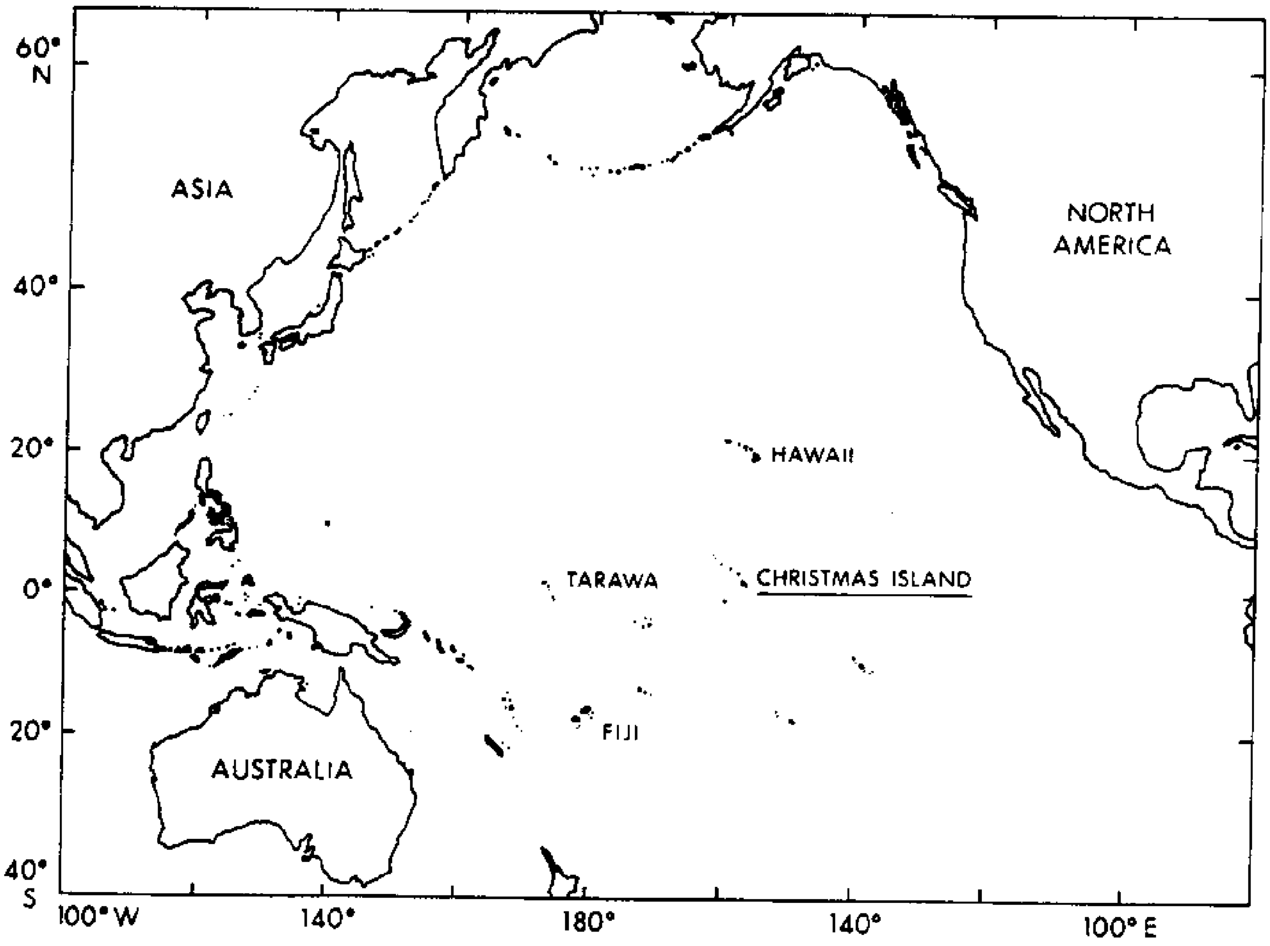

Figure 1. Generalized index map, showing location of Christmas Island, in the Central Pacific Ocean

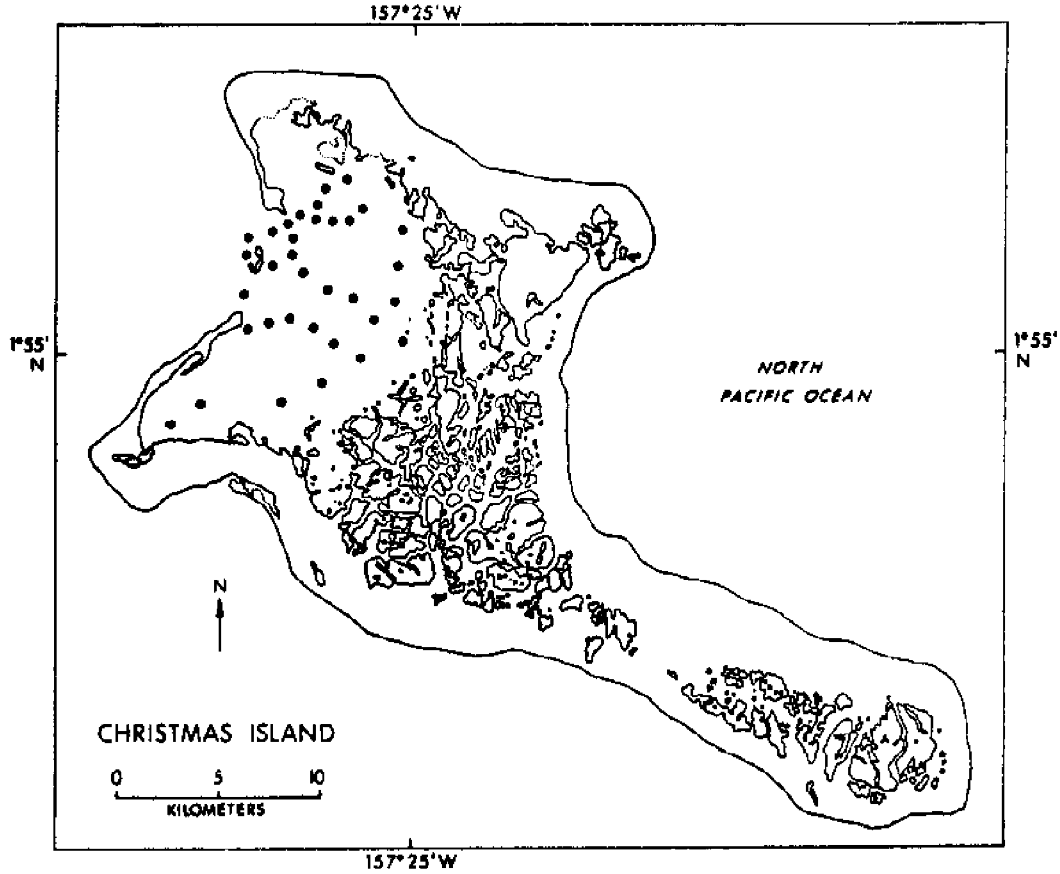

Figure 2. Map of Christmas Island, showing location of lagoon sampling stations

The long-term hypothesis which one of us (S.V. Smith) is pursuing is that rates of material flux in confined bodies of seawater are constrained by relatively simple and recurrent oceanographic factors. These factors are likely to transcend the biological composition of the ecosystem. Generalizations useful to ecosystem analysis and management should emerge from studies such as this one.

Atoll lagoons are convenient environments for pursuit of mass-balance budgets. In comparison with continental or high island embayments, atoll lagoons tend to lack substantial land-derived influences which can complicate data interpretation. Moreover, water often remains in such confined lagoonal systems for fairly long periods of time, allowing local modification of water chemistry by physical, chemical, and biological processes. The rates of modification can be quantified and used as measures of ecosystem function.

Christmas Island has proven to be an interesting and appropriate site for such a study of ecosystem chemistry. General information on the natural history of the atoll is already available (Jenkin and Foale, 1968; Helfrich et al., 1973) and is invaluable to such budgetary analysis. The lagoon of Christmas Atoll is physiographically very similar to two other systems which have been previously studied (Fanning Atoll, Canton Atoll lagoons) and is geographically in close proximity to one of those sites (Fanning). The similarities and differences between Christmas and these other systems have been of particular interest. Meteorological data are critical to such a study, and the available data for Christmas are adequate. Finally, logistic support on Christmas Island was adequate for this study, an important consideration in any environmental study at a remote site.

This report deals primarily with work done in the main lagoon of Christmas Island, with only passing reference to research undertaken on the isolated ponds of the atoll. Work done on the ponds will be covered in more detail in a separate document (Schoonmaker et al., in preparation).

EXPERIMENTAL DESIGN

The "training" aspect of this exercise has been carried over into the writing of this report. Conceptual considerations have been elaborated in more detail here than might otherwise be the case. This editorial decision should increase the value of this report as a model and primer for future surveys of this kind.

Consider the following conceptual model for the changing chemical composition of a water body connected with the ocean (see Smith, 1978, and Smith and Jokiel, 1978, for further discussion and references on this model; Smith and Atkinson, 1983, present a somewhat different version of the same basic calculations for salt and water budgets in confined systems). The chemical composition of that water body largely reflects the oceanic water chemistry, but with some important modifications. Rainfall dilutes the seawater, and evaporation concentrates the sea salts in the water; neither of these alterations does more (for most materials) than adding or subtracting pure water. For the materials examined, we have assumed that any such diluting rainwater is free of significant contaminations with these materials. To the extent that this assumption can be evaluated for unpolluted rainwater in the Central Pacific Ocean, the assumption appears valid.

There may also be input of groundwater or surface runoff from the adjacent land mass; such a water source is likely to have a composition which is significantly different from that of pure water. Both nutrient and alkalinity concentration in groundwater are likely to be elevated substantially above lagoonal levels. Some materials (especially gases which are dissolved in the water or material carried as aerosols) are likely to be exchanged across the air-water surface. Finally, materials may be taken up from the water or released to the water by biological and chemical reactions which occur within the hypothetical water mass. All of these processes are important to water composition within a coral atoll lagoon, and all will be considered in this analysis of Christmas Island.

How long does the water remain in the lagoon? If a steady-state salt concentration is assumed, this property of the system can often be estimated by means of a simple meteorological budget. With this approach, it is assumed that salt advection is balanced by salt diffusion. The rate of salinity change in the lagoon (dS/dt) can be estimated in terms of concentration or dilution by the net effect of evaporation minus rainfall (e-p) in proportion to lagoon depth (z):

$$dS/dt = S \times (e-p)/z \qquad (1)$$

Equation 1 can be rearranged, then solved for salt residence time (t) as a function of salinity change (ΔS) away from oceanic conditions (S_o):

$$t = [z/(e-p)] \times \Delta S/S_o \qquad (2)$$

If freshwater dilution from runoff or groundwater is considered to be a significant term in the water budget, then the "rainfall" term in the above equation would need to be modified to include this additional source of fresh water.

Graphs of salinity versus other chemical components of interest can be used to determine changes which are not due to simple freshwater dilution or concentration. In the simplest instance (dilution by rainfall or concentration by evaporation), the concentration of any material X should change in direct proportion to salinity if the material is conserved with respect to salinity. This proportionality will be denoted the "conservative dilution line."

If material X is taken up or released by processes which are not conservative with respect to salinity, then the observed slope (b) of X versus salinity will differ from the slope of the dilution line (oceanic value of X divided by oceanic salinity). This slope difference can be scaled by depth and the rate of salinity change in order to describe the rate of uptake or release of X per unit area (dX/dt):

$$dX/dt = [(X_o/S_o) - b] \times z \times dS/dt \qquad (3)$$

If the diluting water (rainwater or groundwater) has a significant amount of material X, then the slope of the dilution line is adjusted accordingly. Smith and Pesret (1974) report on a complex example, in which three processes (dilution by rainwater, dilution by compositionally distinct groundwater, and biogeochemical uptake within the system) have been distinguished graphically and algebraically.

This simple procedure for calculating salt residence time from salinity change breaks down at salinities in excess of about 90 o/oo (i.e., about 60 percent of the original water volume has been lost to evaporation), because major contributors to salinity itself ($CaSO_4$) begin precipitating from seawater (see Fernendez et al., 1982). In such an instance, one might use sodium or chloride concentration rather than salinity as a residence time tracer. NaCl or other Na or Cl salts do not precipitate until seawater is evaporated to about 9.5 percent of its original volume ("salinity " ~350 o/oo) (Berner, 1971).

The sampling strategy for such a study emerges from this conceptual model: It is most important to describe the general pattern of salinity distribution in the system and to span the salinity range with other analyses. In the specific case of Christmas Island, samples were therefore collected along transects from the ocean passage to the navigable reaches of the lagoon. This transect survey has then been supplemented with additional samples around the lagoon margin. Sampling of the isolated ponds to the east of the main lagoon has given further insight into the transition between lagoonal processes and processes pertaining to these isolated ponds and the groundwater system of the atoll.

MATERIALS AND METHODS

Water sampling was conducted from small boats throughout the main lagoon of Christmas Island, as well as immediately outside the ocean passage. Sample locations were determined by means of horizontal sextant angles or compass fixes. In order to estimate average water depth of the lagoon, fathometer profiles were run between sampling locations along three transects across the lagoon.

On-site measurements in the lagoon included salinity, temperature, and pH. Salinity and temperature were measured with a Beckman inductive field salinometer at a water depth of 30 cm and at 1-meter intervals throughout the water column. Surface-water pH and temperature were measured with a high-impedance, dual-channel voltmeter equipped with a Sensorex combination electrode and a temperature sensor. Precision on individual measurements was as follows (or better for most measurements): Salinity -- 0.1 o/oo; temperature -- 0.1°C; pH -- 0.005 pH units.

Surface water was collected, immediately pressure-filtered through Whatman GFC filters with syringes equipped with in-line filter holders, then returned to the "laboratory" for analysis of total alkalinity and PO_4. Alkalinity was determined to a precision of at least 0.01 eq m^{-3} with a Corning laboratory pH meter and Sensorex electrode according to procedures described by Smith and Kinsey (1978). PO_4 was measured by standard addition, generally following the techniques of Strickland and Parsons (1972). A Brinkmann colorimeter equipped with a 5-cm fiber optic probe was used; precision was approximately 0.1 mmole m^{-3}. An additional set of filtered samples was collected and subsequently frozen, to be returned to Honolulu for other nutrient analyses on a Technicon autoanalyzer system by HIMB Analytical

Services. Precision was 0.05 mmole m^{-3} or better. Some surface water samples were also collected for laboratory analysis of salinity using a Grundy portable laboratory salinometer (0.01 o/oo). Samples were also collected in glass BOD bottles, poisoned with $HgCl_2$, and returned to Honolulu for processing for ^{13}C analysis.

For the sampling of isolated ponds, salinity was measured (to 1 o/oo) with an American Optical refractometer and subsequently confirmed by laboratory analysis as above. Other procedures for the pond analyses are discussed by Schoonmaker et al. (in preparation).

In addition to the water sampling, selected sediment samples were collected for determination of organic C, N, and P content and for ^{13}C analysis in the inorganic and organic carbon phases. These samples were air dried and returned to Honolulu for further processing. These samples have not yet been processed.

All regression analyses reported herein are geometric mean regressions rather than least squares regressions. As discussed by Ricker (1973) and Laws and Archie (1981), the geometric mean regression is preferred when there is error associated with both variables.

RESULTS AND DISCUSSION

Sampling discussed in this paper was undertaken during a one-week period in mid-July 1983. Table 1 summarizes data on water composition at Christmas Island; Figure 2 shows sample locations. Due to restricted boat availability and difficulty of navigation in some parts of the lagoon, sampling was limited to approximately 30 stations in the main lagoon. This number of samples has proven adequate for the analyses presented here, although it restricts the detail with which the lagoon salinity can be contoured.

Salinity

As discussed above and documented in other studies, salinity patterns in confined water bodies can be used along with meteorological data to establish lagoonal salt and water budgets. These budgets can, in turn, provide a record of water turnover rate, or flushing rate of the lagoonal water mass. Rates of other processes in the system are derived from the salt and water budgets.

Figure 3 illustrates the general salinity pattern throughout the main lagoon. Samples with a salinity greater than 34.5 o/oo are restricted to the vicinity of the passage and are considered to be oceanic in composition. Lagoon salinity varied from 35 o/oo (oceanic) to 28 o/oo in isolated portions of the lagoon and in ponds having some connection with the main lagoon.

TABLE 1. SURFACE WATER COMPOSITION AT CHRISTMAS ISLAND MEAN ± STANDARD DEVIATION (NO. OF OBSERVATIONS).

Property	Ocean	Lagoon
Temperature (°C)	28.1 ± 0.54 (11)	28.6 ± 0.41 (22)
Salinity (o/oo)	34.94 ± 0.16 (11)	31.82 ± 1.34 (22)
pH	8.271 ± 0.021 (11)	8.357 ± 0.117 (22)
Tot. Alk. (eq m^{-3})	2.317 ± 0.047 (10)	2.011 ± 0.062 (22)
Tot. CO_2 (mole m^{-3})	1.929 ± 0.071 (10)	1.650 ± 0.014 (22)
CO_2 partial pressure (µatm)	302 ± 24 (10)	219 ± 42 (22)
Silicon (mmole m^{-3})	2.7 ± 1.0 (11)	3.0 ± 1.3 (22)
Phosphate (mmole m^{-3})	0.32 ± 0.13 (22)	0.14 ± 0.09 (42)
Diss. Org. P (mmole m^{-3})	0.32 ± 0.08 (11)	0.27 ± 0.07 (22)
Nitrate + Nitrite (mmole m^{-3})	2.18 ± 0.85 (11)	0.53 ± 0.51 (21)
Ammonium (mmole m^{-3})	0.53 ± 0.31 (11)	0.40 ± 0.29 (22)
Diss. Org. N (mmole m^{-3})	4.9 ± 1.7 (10)	7.2 ± 1.5 (21)

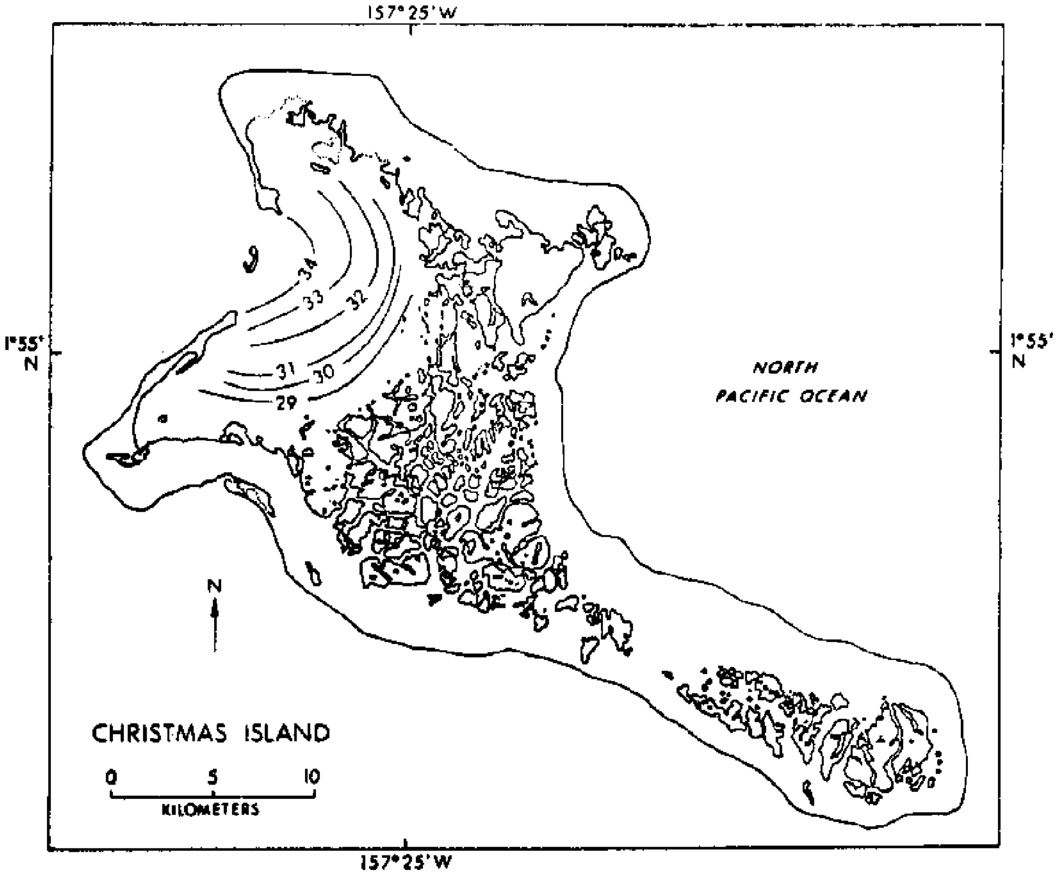

Figure 3. Map of Christmas Island, showing generalized surface salinity contours.

These observations on lagoon salinity can be put into the context of water residence time (Table 2). Rainfall during the period preceding the present survey averaged about 10 mm d^{-1}, and calculated evaporation was about 5 mm d^{-1}, for an average excess freshwater input of about 5 mm d^{-1}. The average lagoon depth is approximately 3m. According to Equation 2, areas with very depressed salinities (about 28 o/oo) have a water age of about 4 months. Mean lagoonal water, with a salinity of about 32 o/oo has an age of about 50 days; the rate of salinity depression is about 0.058 o/oo per day (Equation 1).

TABLE 2. RESIDENCE TIME CALCULATIONS

Meteorological Data	
Rain: (July 1-12) 7.9; (June) 11.4; (May) 6.9; (April) 14.3; (AV.)	10 mm d^{-1}
Humidity: (July only)	84%
Air Temperature: (July only)	27.3°C
Wind: (July only)	4.3 m s^{-1}
Water vapor pressure (from Sverdrup et al., 1942)	38 mbar
Air vapor pressure (from Sverdrup et al., 1942)	30 mbar
Evaporation (July only) (calcs. after Smith and Jokiel 1978)	5 mm d^{-1}
Net freshwater flux	5 mm d^{-1}
Other Variables	
Ocean salinity	34.9 o/oo
Mean lagoon salinity	31.8 o/oo
Minimum lagoon salinity	28 o/oo
Mean lagoon depth	3 m
Salt Residence Time	
Maximum (ΔS = 7 o/oo)	120 days
Mean (ΔS = 3 o/oo)	51 days
Per 1 o/oo ΔS	17 days

All of the above calculations are based upon the assumption that all meteorological flux is accomplished by direct rainfall or evaporation. The island area from which some groundwater might drain into the lagoon is estimated to be perhaps half as large as the lagoon itself; thus freshwater input into the lagoon may be higher than the initial estimate by as much as 50 percent, so that the initial estimate of lagoon water residence time could be too long by as much as one third.

This possible error should be an upper limit on the effect of groundwater flux on the lagoon salinity. Both the pond data and information collected previously (Helfrich et al., 1973) suggest a very steep salinity gradient between ponds which are clearly linked to the lagoonal circulation pattern and adjacent ones which are apparently isolated from the lagoon. If water exchange between groundwater and the open lagoon were large, then there should be more gradual transitions between these water masses.

Data reported here were collected during a period when rainfall was well above the long-term average rates of 2 mm d^{-1} (Taylor 1973). Long-term evaporation at Christmas Island averages 4 mm d^{-1} (close to the estimate of this study; see Jenkin and Foale, 1968), and salinity in the open-water lagoon ordinarily exceeds oceanic values by up to about 3 o/oo (Helfrich et al., 1973). The anomalously high rainfall during the period preceding this expedition should not have significantly biased the estimate of lagoon salt and water residence time; experience with other systems suggests that changing lagoonal salinity with changing rainfall reasonably reflects a constant residence time (Smith and Pesret, 1974; Smith and Jokiel, 1978).

Carbon Dioxide

Carbon dioxide is a useful tracer of major biogeochemical and physical processes occurring in isolated water bodies. CO_2 is involved in two important biogeochemical processes: organic carbon metabolism and $CaCO_3$ reactions; CO_2 is also involved in gas transfer across the air-sea interface. Hence, graphs of CO_2 versus salinity illustrate that CO_2 does not fall along the "conservative dilution line." Rather, the values are deflected below that line; there is a record of net CO_2 uptake in systems such as atoll lagoons.

The pH and total alkalinity data can be used to calculate total CO_2 content and CO_2 partial pressure of the lagoon water (see Smith and Atkinson, 1983, for a comprehensive discussion and other citations). Figures 4, 5, and 6 and Table 1 illustrate the change of total alkalinity, total CO_2, and CO_2 partial pressure as functions of salinity. Several generalities emerge. As lagoon water ages (i.e., during the present survey, became less saline), both total CO_2 and total alkalinity decrease below the line which would result from dilution by fresh water. Clearly both total CO_2 and total alkalinity are being taken out of the water by processes acting on the lagoon chemistry.

Uptake of total alkalinity is a direct consequence of the precipitation of $CaCO_3$ (in this system, by biological activity), and uptake of total CO_2 reflects the summation of $CaCO_3$ precipitation, organic carbon production, and CO_2 gas exchange across the air-water interface. The partitioning of CO_2 flux to and from the water among these three processes will be described.

The total CO_2 loss from the water is denoted as T. There is little reason for direct interest in T, but this value is needed to solve algebraically for other processes of CO_2 flux.

CO_2 loss from $CaCO_3$ precipitation (C) equals half the loss in total alkalinity. The rate of this process is of fundamental interest, because it is related to the rate of coral reef growth and can be compared with $CaCO_3$ production and sedimentation rates in other systems.

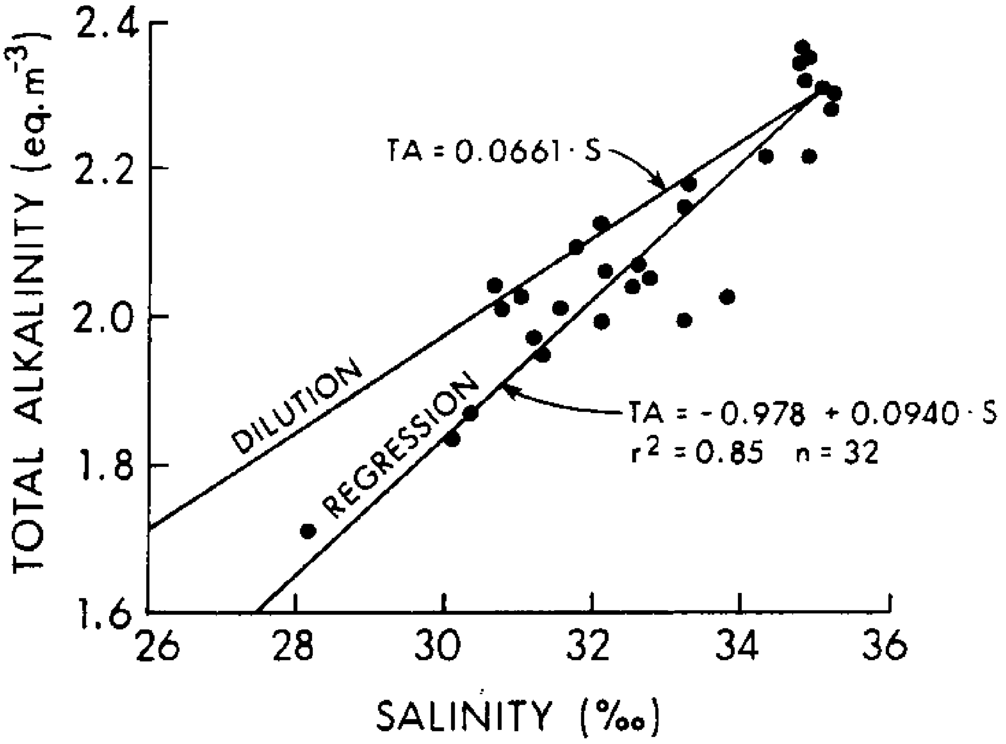

Figure 4. Total alkalinity as a function of salinity. The difference in slope between the "dilution line" and the regression line is a measure of total alkalinity uptake in the lagoon. Total alkalinity uptake divided by 2 is a measure of the CO_2 uptake by $CaCO_3$ production.

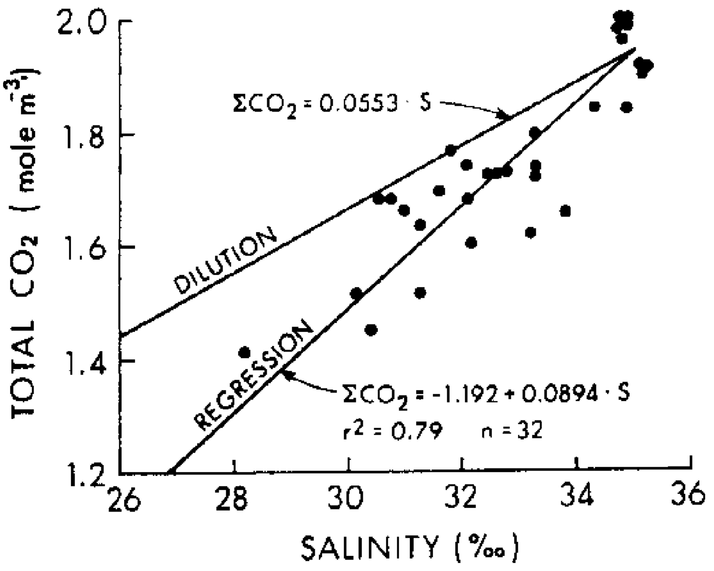

Figure 5. Total CO_2 as a function of salinity. The difference in slopes between the "dilution line" and the regression line is a measure of CO_2 uptake in the lagoon. Processes of CO_2 uptake include $CaCO_3$ production, organic carbon production, and gas transfer. The partitioning among these processes is discussed in the text.

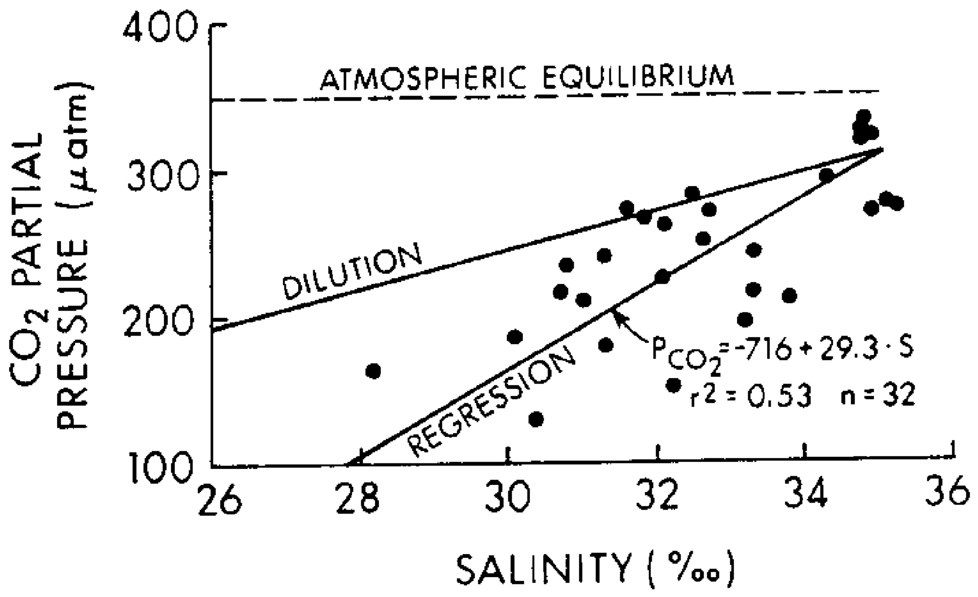

Figure 6. Change in CO_2 partial pressure as a function of salinity. Note that water enters the lagoon near atmospheric equilibrium. The "dilution line" for CO_2 partial pressure is not derived via simple proportionality, as has been done for other materials. Rather it is the partial pressure calculated if both CO_2 and alkalinity are diluted conservatively with respect to salinity. The low CO_2 partial pressure of lagoon waters indicates that CO_2 will diffuse from the air into the water.

Gas exchange (G) can be calculated as the product of the solubility (α) of CO_2 gas in water of specified temperature and salinity, a gas exchange rate coefficient (K), and the difference in CO_2 gas pressure between the water column and the overlying atmosphere (ΔP):

$$G = \alpha \times K \times P \qquad (4)$$

Gas flux is of importance to the global chemistry of CO_2; at the scale of individual ecosystems, however, it is simply a correction which must be applied inorder to solve for those processes of CO_2 flux of more direct utility to interpretation of ecosystem function.

The remaining process accounting for significant CO_2 flux is organic metabolism (O), either net production or net consumption of organic compounds. The three processes of CO_2 flux accounting for T can be represented by a simple summation:

$$T = C + G + O \qquad (5)$$

Then Equation 5 can be rearranged and solved for CO_2 uptake due to organic metabolism (O):

$$O = T - C - G \tag{6}$$

Table 3 summarizes the results of calculations according to the procedures which are outlined above. $CaCO_3$ precipitation (C) consumes 2.5 mmole CO_2 m^{-2} d^{-1}; this rate of CO_2 uptake is equivalent to a $CaCO_3$ precipitation rate of about 90 g $CaCO_3$ m^{-2} yr^{-1}, a very slow rate in comparison with that of other atoll lagoons for which there are available data (Table 4). In fact, this rate is not much more rapid than typical open-ocean $CaCO_3$ production rates.

TABLE 3. CO_2 FLUX CALCULATIONS

Total CO_2 Change (T)	
Dilution-induced CO_2 change (Figure 5)	-0.0553 mole m^{-3} o/oo^{-1}
Observed CO_2 change (Figure 5)	-0.0894
Non-conservative CO_2 change (Equation 3)	-0.0060 mole m^{-2} d^{-1}
Calcification-induced CO_2 Change (C)	
Dilution-induced alkalinity change (Figure 4)	-0.0661 eq m^{-3} o/oo^{-1}
Observed alkalinity change (Figure 4)	-0.0940
Non-conservative alkalinity change (Equation 3)	-0.0049 eq m^{-2} d^{-1}
CO_2 change (divide previous slope by 2)	-0.0025 mole m^{-2} d^{-1}
CO_2 Gas Flux (G)	
CO_2 solubility in seawater (from Weiss, 1974)	26 mole m^{-3} atm^{-1}
Exchange rate coefficient (Smith and Atkinson, 1983)	0.5 to 1.0 m d^{-1}
Pressure deviation below equilibrium (Figure 6)	130×10^{-6}
Gas flux (Equation 2)	0.0017 to 0.0034 mole m^{-2} d^{-1}
Organic metabolism (O)	
(Equation 6)	-0.0052 to -0.0069 mole m^{-2} d^{-1}

Note: Details of calculations are explained in the text

TABLE 4. COMPARISON OF NET INORGANIC AND ORGANIC CARBON FLUX IN THE CHRISTMAS ISLAND LAGOON WITH FLUXES IN OTHER CONFINED WATER BODIES

$CaCO_3$ Flux

LOCATION (Reference)	Rate ($g\ CaCO_3\ m^{-2}\ yr^{-1}$)	Comments
Fanning 1972 (Smith and Pesret, 1974)	1000	Atoll lagoon
Canton (Smith and Jokiel, 1978)	500	Atoll lagoon
Bahamas (Broecker and Takahashi, 1966)	500	Carbonate shoals
One Tree (Kinsey 1979)	500	Atoll lagoon
Fanning 1983 (Smith et al., in preparation)	400	Atoll lagoon -- compare with 1972
Shark Bay (Smith and Atkinson, 1983)	120	Hypersaline bay
Christmas (this study)	90	Atoll lagoon

Organic Carbon Production

LOCATION (Reference)	Rate ($mg\ C\ m^{-2}\ d^{-1}$)	Comments
Canton (Smith and Jokiel, 1978)	170	Recalculated using Equation 4 and $K = 0.5$ to 3.0
Christmas Island (this study)	70	Complete CO_2 budget
Shark Bay (Smith and Atkinson, 1983)	15	Complete CO_2 budget
Fanning 1983 (Smith et al., in preparation)	0	Complete CO_2 budget
Fanning 1972 (Smith and Pesret, 1974)	-10	Done same as Canton

Two alternative explanations can be put forward to account for this observation of very low $CaCO_3$ production; which of the two is correct cannot be resolved with available data. $CaCO_3$ production, and presumably reef construction, may ordinarily be a very minor activity in the lagoon of Christmas Island. Depressed rates of $CaCO_3$ production may well be a late stage in the normal evolution of an atoll lagoon during infilling. Although live corals and other calcifying organisms in the lagoon were observed, the observations were insufficient to assess the quantitative importance of these organisms to the system.

Alternatively, calculations from data collected during the present survey may represent an anomalous situation, perhaps somehow brought about by the "El Niño" conditions which have been affecting the Central Pacific Ocean since late 1982. There is evidence (Smith et al., in preparation) of depressed $CaCO_3$ production in the lagoon of nearby Fanning Atoll. Moreover, some corals on the Christmas Island lagoonal reef flats appear to have been killed, perhaps by the rise and subsequent fall in sea level accompanying this El Niño event (K. Wyrtki, 1983: personal communication).

Average CO_2 partial pressure in the lagoon waters is about 220 μatm, 130 μatm below atmospheric equilibrium (Figure 6). The average wind speed during the present survey was about 4 m s^{-1} (Table 2); it can be estimated from Smith and Atkinson (1983) that the gas transfer coefficient (K) at this speed lies between 0.5 and 1 m d^{-1}. The solubility (α) of CO_2 gas in water of 32 o/oo and 28°C is approximately 26 mole m^{-3} atm^{-1} (Weiss 1974). It follows from Equation 4 that gas flux (G) delivers 1.7 to 3.4 mmole m^{-2} d^{-1} to the water.

Finally, organic carbon production (O) is calculated according to Equation 6 to remove between 5.2 and 6.9 mmole CO_2 m^{-2} d^{-1} (an average of 6.0 mmole m^{-2} d^{-1}). This average value is equivalent to a net organic carbon production rate of about 70 mg C m^{-2} d^{-1}.

It is possible to put these data into the context of limited additional information for other systems. Calculations by Smith and Pesret (1972) for Fanning Atoll and by Smith and Jokiel (1978) for Canton have been revised to reflect an increased confidence in estimating the gas transfer coefficient (based on assumed tradewind speeds of up to 7 m s^{-1} and the data summary of Smith and Atkinson [1983] for K). Equation 6 is used to solve for organic metabolism.

Table 4 reflects the results. Clearly there is a fair range of net production rates for such large, confined ecosystems, with Christmas Island falling in the middle of this range. It will follow from the discussion on nutrient flux that we believe the net organic carbon production of such confined systems to be largely set by phosphorus supply.

The Christmas Island lagoon, like other coral reef systems which have been examined, consumes virtually all of the carbon it produces. There is no evidence of significant organic carbon export, nor is there need for an external supply of organic carbon to meet the metabolic requirements of the system.

One is tempted to speculate on the implications of such an apparently low net production rate to a local fishery. The answer, although necessarily incomplete and speculative, is interesting. The lagoon area is approximately 180 km^2, so even this "low production" amounts to a net lagoon-wide production of about 5000 metric tons of organic carbon per year. This figure seems far in excess of any rational expectation of fisheries yield for the lagoon, implying that many other factors besides net ecosystem production of organic carbon limit the resulting fisheries. Resource partitioning among trophic levels and commercially acceptable fisheries within the system must provide at least part of the answer.

An ecosystem budgetary model calculated by Polovina (1983) for French Frigate Shoals (Northwest Hawaiian Islands) suggests that third trophic level organisms, from which most harvestable organisms are likely to be derived, account for about 1 percent of the net production of that particular reef system. If it is assumed that 10 percent of that production is both commercially acceptable and might be harvested without serious impact upon the system, then the net fisheries yield of the Christmas Island lagoon might be anticipated to be of the order of 5 tons carbon, or 100 tons (wet weight) per year.

The importance of these calculations is not to provide an estimate of the potential fisheries yield for the Christmas Island lagoon. Rather, it is to stress that resource partitioning, not net production, must limit this potential yield. Highly diverse systems like coral reefs partition the resources among many compartments, lowering their likely yield: production ratio well below that of less diverse systems. This hypothesis bears further investigation.

Nutrients

Three inorganic plant nutrients are generally considered to be important to the function of marine ecosystems: phosphorus, nitrogen, and silicon. The uptake or release of these materials can impart substantial chemical signals on the water composition, and the availability of these nutrients can, in principle, limit the growth rate of individual organisms or the organic carbon accumulation of the entire system.

It is worth noting that the nutrients, because of their low concentration and high demand in ecosystems with a large biomass and likely high production, are involved to a large extent in active uptake and release -- ecosystem cycling. This cycling may well account for much of the scatter, or "noise," which one observes in almost any set of environmental nutrient data (see Imberger et al., 1983, for an elegant mathematical treatment of this point).

However, in a study such as this one, the interest is in the trends of net nutrient uptake or release which must be superimposed upon such scatter if the system is engaged in any physical, chemical, or biological processing of these materials beyond strict turnover. Recycling may well be important to the details of ecosystem function, and such recycling is usefully studied at the level of the communities or organisms accounting for it. However, recycling of nutrients cannot sustain net ecosystem accumulation (growth).

First, consider (and rapidly dismiss) silicon (Figure 7; Table 1). There is no clear trend in Si as a function of salinity. A similar lack of pattern for Si versus salinity was observed in the lagoon of Canton Atoll (Smith and Jokiel, 1978). This result is not surprising. Silicon is not required for the growth of most marine organisms (see, e.g., Webb, 1981). Diatoms, sponges, and other organisms requiring silicon are present but not abundant in reef ecosystems, and remains of these organisms are very rare in reef sediments. There is not significant net utilization of Si by this ecosystem, or probably by most other coral-reef systems.

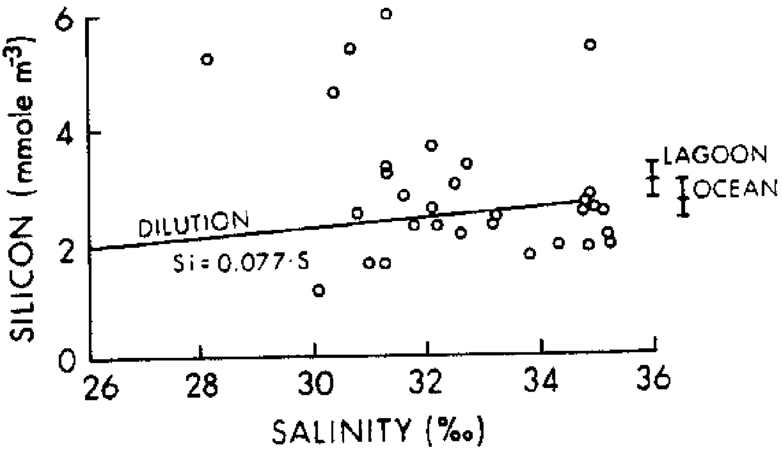

Figure 7. Silicon as a function of salinity. The lack of difference between lagoonal composition and the "dilution line" indicates that there is no significant uptake or release of silicon. Ocean and lagoon Si values (mean, standard error) are shown by the vertical bars.

Phosphorus is present in the water in two major forms: PO_4 and dissolved organic phosphorus (DOP). Graphs of these two constituents as functions of salinity are illustrated in Figures 8 and 9 (see also Table 1). Because PO_4 has proven elsewhere to be valuable indicator of net ecosystem metabolism (Smith and Jokiel, 1978; Atkinson, 1981; Smith and Atkinson, 1983), this particular nutrient was measured in the field laboratory; samples were also returned to Honolulu for subsequent re-analysis. Both sets of data are shown in Figure 8.

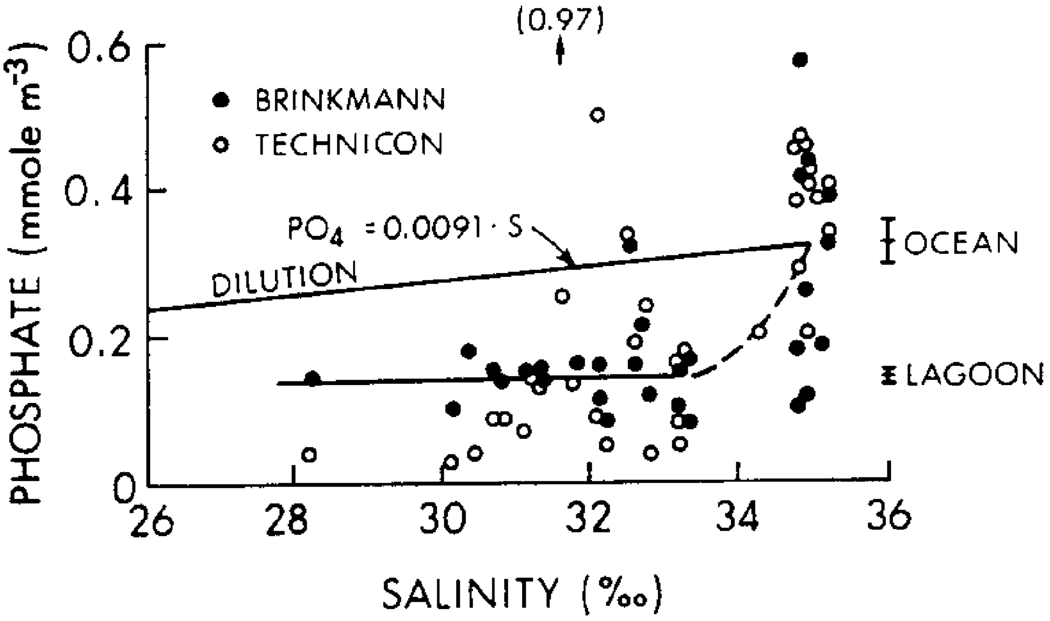

Figure 8. Phosphate as a function of salinity. Phosphate is taken up most rapidly in water of near-oceanic salinity, then cycled within the remainder of the system with no net uptake or release. The one value at 0.97 mmole m^{-3} has been excluded from the analysis. Ocean and lagoon PO_4 values (mean, standard error) are shown by the vertical bars. Data measured in our field laboratory with a Brinkmann colorimeter have been pooled with data from frozen samples which were returned to Honolulu for analysis with a Technicon autoanalyzer.

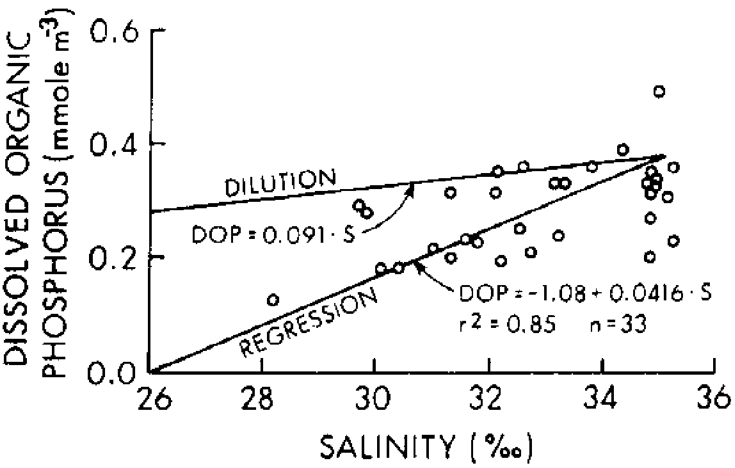

Figure 9. Dissolved organic phosphorus as a function of salinity. The difference in slopes between the "dilution line" and the regression line is measure of DOP uptake in the lagoon.

As indicated by that figure, PO_4 is relatively abundant in ocean water and drops rapidly to a much lower average lagoon level. The difference between the oceanic and lagoon PO_4 levels is statistically highly significant. The non-linearity of PO_4 change with respect to salinity has been observed in other confined systems (Smith and Jokiel, 1978; Smith and Atkinson, 1983) and appears to represent rapid uptake of PO_4 near the entrance to the lagoon.

Because these data do not show the linear trends which have been illustrated by the CO_2 data, uptake rates have been calculated in a slightly different fashion: the mean decrease in PO_4 between the ocean and lagoon (0.18 mmole m^{-3}) divided by the mean lagoon water residence time (50 days) and multiplied by water depth (3 m) is a measure of the PO_4 uptake rate (0.011 mmole m^{-2} d^{-1}) averaged throughout the whole system. (Note, however, the argument that this average probably represents rapid uptake near the lagoon entrance and little net uptake elsewhere.)

Dissolved organic phosphorus (DOP) decreases linearly as salinity decreases (Figure 9). The dilution-corrected slope multiplied by the rate of salinity change and the water depth yields a DOP uptake rate of 0.006 mmole m^{-2} d^{-1}. Previous phosphorus budgets of this kind (Smith and Jokiel, 1978; Smith and Atkinson, 1983) have either left DOP out of the budget or have calculated that it is not a significant term. At least in the case of Christmas Island, this term appears to account for about 35 percent of the total phosphorus taken up from ocean water entering the system. The net uptake rate of P supplied from the ocean is thus 0.017 mmole m^{-2} d^{-1}.

Another source of phosphorus merits consideration. Christmas Island has a large population of seabirds. These birds feed at sea but return to the island to nest -- and to defecate. Table 5 summarizes data supplied by R. Schreiber (personal communication, 1983) and Schreiber and Ashmole (1970). An interesting result emerges. Under ordinary conditions, the possible contribution of the birds to the lagoon phosphorus budget would be quite large. However, apparently due to the "El Niño" conditions which are also presently accounting for the unusually high rainfall, the bird population on Christmas Island and their potential contribution to the local phosphorus budget have been reduced to about 1 percent of the normal value. This flux is apparently insignificant.

TABLE 5. POTENTIAL CONTRIBUTION OF SEABIRDS TO CHRISTMAS ISLAND P BUDGET

Bird numbers nesting on island	
Usual population	10^7 birds
1983 population	10^5 birds
Nesting time on the island	20% per year
Assumed bird biomass	
Wet weight	200 g $bird^{-1}$
Dry weight	20 g $bird^{-1}$
Assumed food composition (based on plankton)	0.3 mmole P g dry^{-1}
Assumed daily food turnover (% of body weight)	25% d^{-1}
Phosphorus flux	
Daily turnover in food	1.5 mmole $bird^{-1}$
Prorated for nesting time	0.3 mmole $bird^{-1}$
Prorated for number of birds	
Usual	0.3 x 10^7 mmole d^{-1}
1983	0.3 x 10^5 mmole d^{-1}
Prorated for lagoon area (180 km^2)	
Usual	0.02 mmole m^{-2} d^{-1}
1983	0.0002 mmole m^{-2} d^{-1}

Source: Data and estimates from R. Schreiber, 1983: personal communication; Schreiber and Ashmole, 1970

Note: These fluxes are upper bounds, based on the assumption that the entire production of guano is delivered to the lagoon. The actual delivery of P is unknown.

There could, of course, be a lag between the time of guano accumulation on land during dry periods and transport to the lagoon during periods of high rainfall. There is no evidence of such a phenomenon, from either the phosphorus levels of low-salinity water in the lagoon or the phosphorus content of the low-salinity ponds of the atoll (Schoonmaker et al., in preparation). Although some soils on the island are somewhat enriched in phosphorus in apparent response to some guano accumulation, there do not seem to be any significant phosphorite deposits on the atoll (Jenkin and Foale, 1968; Valencia, 1977). If such deposits were abundant on the atoll, they might provide a significant, lagged phosphorus leak into the lagoon during periods of high rainfall. That does not seem to be the case.

The calculation of potential seabird contribution to the lagoonal P budget must be regarded as an upper limit, because it is not known how much of the guano might actually reach the lagoon. There is no way, from available data, to assess the real contribution of the birds to the lagoon phosphorus budget under normal rainfall conditions. The possibility that this nutrient source may sometimes be important is an interesting one that merits future consideration.

Smith and Atkinson (1983) have presented in some detail arguments as to why phosphorus uptake can be viewed as a measure of organic metabolism, although an alternative view (e.g., deKanel and Morse 1978) would favor direct adsorption of phosphorus onto the surfaces of carbonate sediments. Let us compare the net phosphorus uptake with our calculations of organic carbon production. This comparison is readily obtained from the calculated organic C:P uptake ratio of 350:1. This ratio is in the range of organic C:P ratios commonly found in benthic plants (Atkinson and Smith, 1983).

Carbonate sediments typically have an organic C:P ratio of about 300:1 (Smith and Atkinson, in press; also calculable from data in Berner, 1982, plus Froelich et al., 1982). We suggest that his ratio apparently reflects the net storage ratio of organic materials in the sediments after selective release of C, regardless of the initial uptake ratio. Perhaps the ratio is controlled by oxidation of organic material, coupled with P adsorption to the carbonate surfaces. Some such model would be generally consistent with both the "carbonate adsorption" and the "organic uptake" models of P uptake from the water. The use of P uptake as a measure of organic carbon metabolism remains a reasonable, although by no means proven, model. Further evidence will be provided below.

Figures 10, 11, and 12 and Table 1 summarize the nitrogen data. The forms of nitrogen most readily available for plant uptake include NO_3, NO_2 (these first two are commonly measured together and simply reported as NO_3, the dominant form), and NH_4. Dissolved organic nitrogen (DON) is by far the most common form of fixed nitrogen in seawater, but except for the urea fraction and some amino acids, DON compounds are not readily available to the biological community (McCarthy, 1972).

NO_3 (Figure 10) shows a pattern very much like PO_4: it drops rapidly from oceanic levels to a substantially lower lagoonal average. The calculated lagoonal uptake rate of NO_3 is 0.10 mmole m^{-2} d^{-1}, about nine times the PO_4 uptake rate. By contrast, there is no evidence of NH_4 uptake (Figure 11).

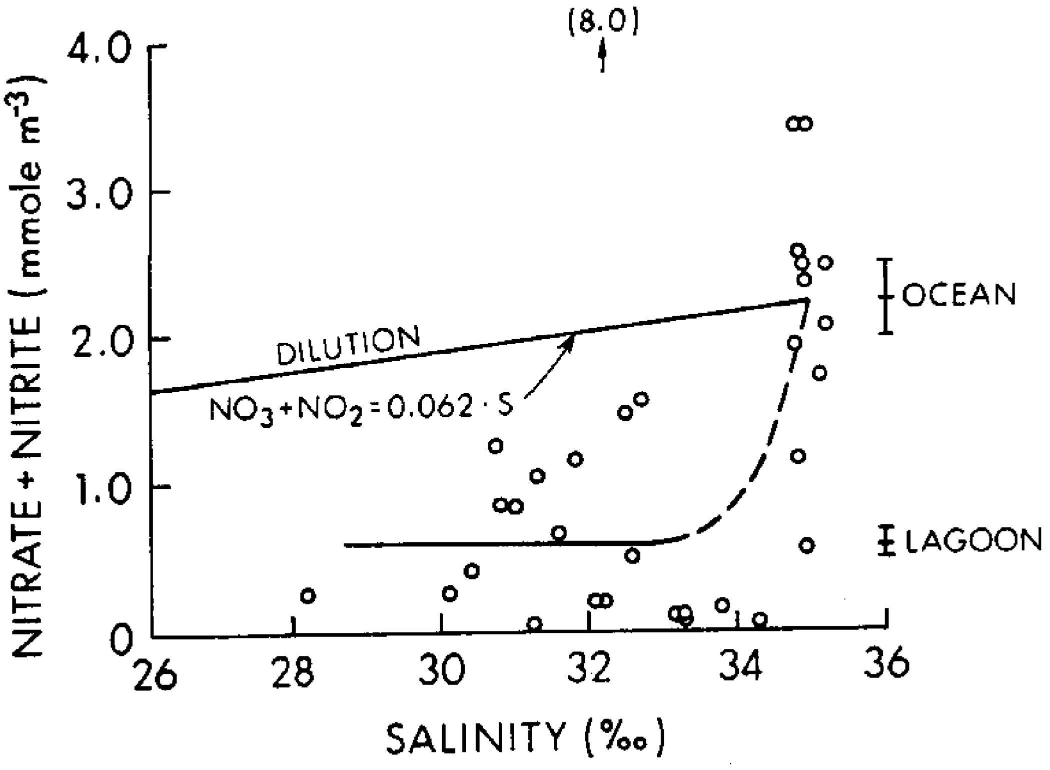

Figure 10. Nitrate plus nitrite as a function of salinity. These forms of N are taken up most rapidly in water of near-oceanic salinity, then cycled within the system with no net uptake or release. The value at 8 mmole m^{-3} has been excluded from the analysis. Ocean and lagoon NO_3 + NO_2 values (mean, standard error) are shown by the vertical bars.

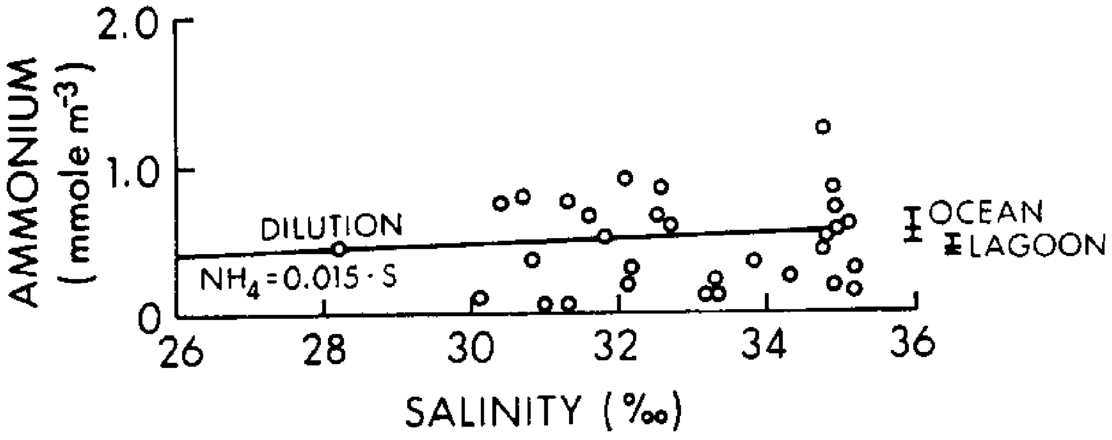

Figure 11. Ammonium as a function of salinity. The lack of difference between lagoonal composition and the "dilution line" indicates that there is no significant net uptake or release of ammonium. Ocean and lagoon NH_4 values (mean, standard error) are shown by the vertical bars.

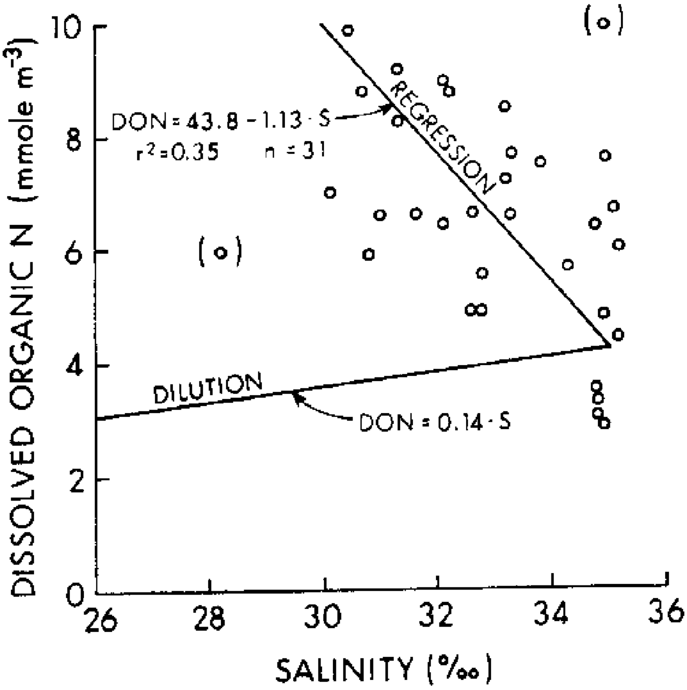

Figure 12. Dissolved organic nitrogen as a function of salinity. The two values in parentheses have been treated as outliers and excluded from the regression analysis. The steep negative slope indicates that there is some source of DON within the lagoon, and that DON is being exported.

The relationship between inorganic nitrogen and inorganic phosphorus uptake is also usefully examined by a graph of these two variables plotted against one another (Figure 13). The net concentration ratio of inorganic N:P is 8.2, close to the ratio derived from the average NO_3 and PO_4 uptake rates. The fact that the concentration of dissolved inorganic nitrogen and phosphorus correlate well with one another is persuasive evidence that the documented PO_4 uptake proceeds via organic production rather than adsorption of PO_4 onto carbonate surfaces. There is, to our knowledge, no suggestion in the literature that such adsorption occurs for inorganic nitrogen, and the strong correlation between the two variables is most readily explained by a common uptake mechanism.

This uptake ratio is interesting for another reason: it is similar to the uptake ratios reported by Smith and Jokiel (1978) at Canton Atoll and by Kimmerer and Walsh (1981) at Tarawa Atoll; yet this ratio is dramatically different from the N:P ratio of 30:1 which typifies the composition of benthic plants (Atkinson and Smith, 1983). Ryther and Dunstan (1971) suggest that the ideal uptake ratio into plankton is about 10:1; despite this

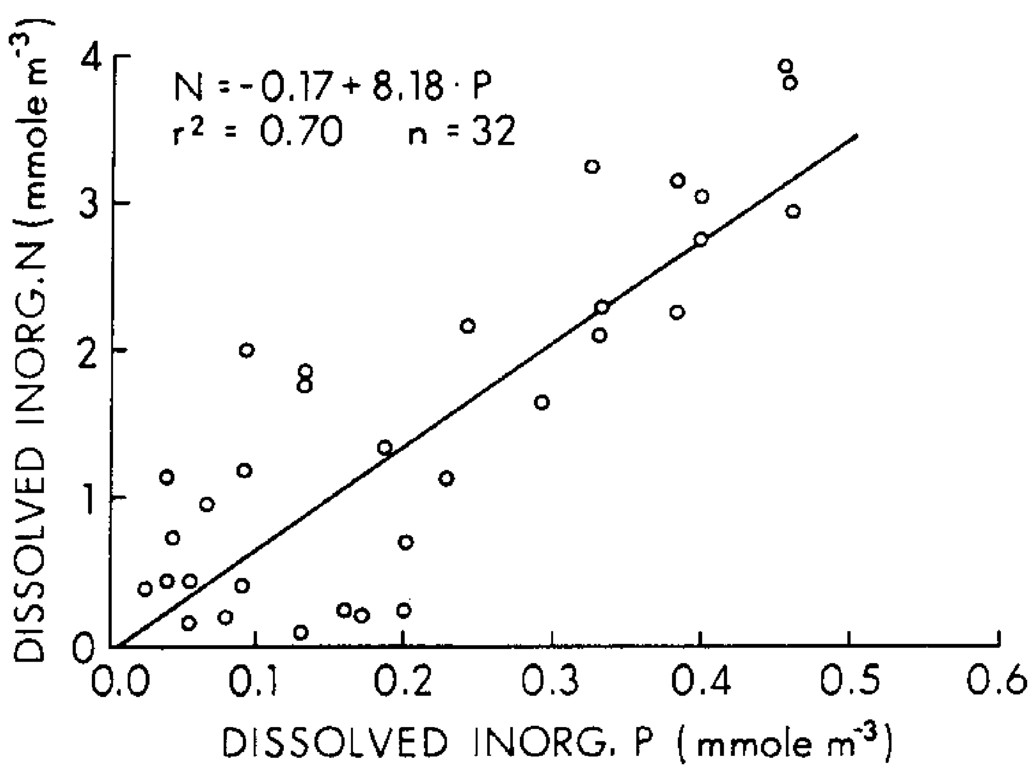

Figure 13. Dissolved inorganic nitrogen versus dissolved inorganic phosphorus concentration in lagoonal waters. The slope of this line represents the apparent net uptake ratio of these materials. Note that the Y intercept of this regression line does not differ significantly from 0, indicating that the two nutrients are simultaneously exhausted.

similarity of apparent N:P uptake ratios in atoll lagoons with an ideal plankton uptake ratio, we do not believe that the net production of Christmas Island is dominated by plankton. Nor do we believe that this low ratio is indicative of nitrogen limitation in these systems. These points will be discussed further.

The DON pattern (Figure 12) is markedly different from all other materials examined: DON clearly increases with decreasing salinity, so there must be DON production in the lagoon and export from it. One might suspect that the inorganic nitrogen has been converted to DON and is being exported. However, the calculated DON production rate of 0.22 mmole m^{-2} d^{-1} is over twice the uptake rate of inorganic nitrogen. There must be another source of DON.

Webb et al. (1975) reported a large production and export of DON on the reef flat of Enewetak atoll, and Wiebe et al. (1975) demonstrated that this phenomenon could be attributed to rapid biological fixation of free nitrogen. Rapid nitrogen fixation has subsequently become regarded as a widespread phenomenon of coral reefs (Wiebe, 1976; Capone, 1977). We suggest that nitrogen fixation accounts for the observed DON efflux from the Christmas Island lagoon and probably also accounts for the apparent discrepancy between net inorganic N:P uptake ratios and the composition of benthic plants.

The DON flux which Webb et al. (1975) measured greatly exceeded the flux observed for the entire lagoonal system of Christmas Island. Wiebe et al. (1975) calculated a nitrogen fixation rate of 13 mmole m^{-2} d^{-1}. The observed system-wide rate of net DON production can easily be accounted for by nitrogen fixation. For a coral reef-flat transect with no net organic carbon production (Smith and Marsh, 1973) or phosphorus uptake (Pilson and Betzer, 1973), Webb et al. (1975) observed that about 37 percent of the fixed nitrogen export was DON. We therefore suggest that the observed DON production rate of 0.22 mmole m^{-2} d^{-1} implies an "internal" source of nitrogen (i.e., nitrogen fixation) amounting to perhaps 0.6 mmole m^{-2} d^{-1}. This apparent fixation rate is only about 5 percent of the rate estimated for reef flats. About 0.4 mmole m^{-2} d^{-1} would be inorganic nitrogen. Therefore the estimated N uptake is about 0.5 mmole m^{-2} d^{-1}, so the true N:P uptake ratio is apparently about 29:1. This value is close to the average value reported for benthic plants (30:1; Atkinson and Smith, 1983).

About 80 percent of the inorganic nitrogen taken up by the ecosystem appears to come from nitrogen fixation, not oceanic import. Just enough N is fixed to use up available P; thus the observed apparent N:P uptake line (Figure 13) has a slope representing the oceanic delivery ratio and passes through the origin of the graph.

Directly measuring local nitrogen fixation by incubation techniques in a few arbitrary, and probably not particularly representative, environments would not provide much information beyond the ecosystem-wide budget calculated here. Nitrogen fixation is certainly a well-accepted characteristic of many marine environments (e.g. Capone and Carpenter, 1982), and the fixation rate estimated here is very low in comparison to nitrogen fixation in some reef communities. This rate could increase substantially in the Christmas Island lagoon if the system had sufficient phosphorus to support higher net organic carbon production.

Canton Island, a coral atoll with a lagoon superficially similar to Christmas, has a more rapid phosphorus delivery rate (Smith and Jokiel, 1978) and clearly produces more organic carbon (Table 4). We suggest, therefore, that the net production of organic material by confined systems such as these atoll lagoons is limited by the availability of phosphorus, not nitrogen.

Schindler (1977) has argued that lakes, which are another example of confined water bodies capable of accumulating fixed nitrogen, also tend to be phosphorus limited. Smith and Atkinson (in press) have suggested this to be a general characteristic of biological communities in confined water bodies. This situation for confined water bodies is in apparent contrast to the generally accepted view that open coastal water bodies are nitrogen-limited (Ryther and Dunstan, 1971).

CONCLUSIONS

It appears to be a characteristic of confined water bodies that they will exhaust their supply of certain nutrients present in potentially limiting concentrations. The net rate of nutrient uptake leading to this exhaustion will be oceanographically constrained -- and slow.

Two nutrients seem destined to be exhausted in such systems: nitrogen and phosphorus. Under these circumstances of confinement, any deficit in nitrogen is likely to be met by nitrogen fixation. It appears inevitable that phosphorus, not nitrogen, will limit the net production of organic materials within the system.

Any reasonable scaling of net phosphorus supply and uptake to CO_2 uptake demonstrates that net organic carbon production in such confined water bodies must be small. This situation contrasts markedly with the uptake dynamics of communities in flowing water. These communities have a large supply of advected nutrients (Atkinson, 1981). This supply is not significantly depleted by uptake (Pilson and Betzer, 1973), so the systems can only be nutritionally limited by concentration. The net metabolism of confined water bodies is limited by both concentration and supply of nutrients.

An apparent, not unexpected corollary to this conclusion is the observation that net uptake of nutrients in such a confined system is most rapid near the site where the nutrients enter the system. It seems likely, although by no means proven from the data, that both the growth rate of individual organisms and the total abundance of organisms will be highest near the site of nutrient input. Communities progressively removed from the site of nutrient input will be progressively constrained to turnover, rather than net uptake, of materials. Evidence from another confined system (Shark Bay, Smith and Atkinson, 1983) suggests that gross production under these circumstances is not directly nutrient limited.

It does not necessarily follow from the above observations that increased water flow through such confined systems would proportionally enhance their biological yield. All else being equal, greater water throughput will supply more nutrients, some of which may be taken up. However, this increased throughput may also wash out both unprocessed nutrients and organic products without effective processing within the system. These confined systems may be particularly efficient in converting organic products to biomass rather than losing the organic material into detrital pools.

The timespan covered by this study is clearly very restricted. Nevertheless, in terms of the variety of materials examined, this study is one of the more comprehensive mass balances of biologically active materials in a confined marine water body. It is entirely possible that some of the absolute rates which have been calculated are influenced by unusual weather conditions or have other viases inherent in such one-time expeditionary studies. Indeed, that possibility is suggested in the case of the calculated rates of $CaCO_3$ production. Nevertheless, further study of such confined water bodies may offer unusual insight into the flux of biologically active materials through ecosystems.

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