WATER COMPOSITION AND BIOGEOCHEMICAL GRADIENTS IN THE CANTON ATOLL LAGOON*

by

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and

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ABSTRACT

Budgets of water, salt, nutrients, carbon dioxide, suspended material, and sediments can be used to establish the dynamics of water exchange, biogeochemical reactions, and sedimentation in the Canton Atoll lagoon.

Maximum water residence time in the lagoon is about 95 days. During that time, net evaporation raises the salinity nearly 4 $^{o}/oo$ above oceanic values. Phosphorus utilization in the lagoon is 0.027 mmole m^{-2} day^{-1}; nitrogen utilization is about 8.5 times this rate. Net excess organic carbon production is assumed to be 100 times the rate of phosphorus utilization (that is, about 3 mmoles m^{-2} day^{-1}, or 36 mg C m^{-2} day^{-1}). Gross production, as inferred from gas exchange between the air and water, is 6 g C m^{-2} day^{-1}. $CaCO_3$ production is 14 mmoles m^{-2} day^{-1}, or 1.4 g $CaCO_3$ m^{-2} day^{-1}. Most of the $CaCO_3$ produced in the lagoon remains there, but a substantial portion of the organic carbon produced is lost from the lagoon.

Water motion is the parameter exerting major influence on the metabolism of the lagoon biotic community. Artificial alteration of water movement patterns has changed part of that community. Neither nitrogen nor phosphorus is likely to limit metabolism of the biota. $CaCO_3$ production in the lagoon has probably been sufficient to fill the lagoon with about 20 m of sediment over the past 8,000 years. It is likely that the present episode of lagoon reef growth has been continuing for that timespan and that the $CaCO_3$ production rate has decreased substantially over that period.

ACKNOWLEDGMENTS

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INTRODUCTION

Coral atolls have long been recognized for their variety, complexity, and fertility in the midst of an oceanic "desert." Most studies of reef systems have primarily considered their composition, with little regard for the dynamic balance of material production, utilization, and removal. Yet the ability of coral reefs to grow and maintain themselves near sea level over millenia is surely their most conspicuous attribute. This growth results from both $CaCO_3$ production and associated organic carbon metabolism by countless organisms inhabiting the coral reefs.

Calcium carbonate production by coral reefs has been estimated by several investigators over the past century (for a recent review, see Chave *et al.*, 1972). The estimates have been made for individual organisms, for portions of reefs, and for entire reef systems. Some recent studies have departed from the traditional approach of estimating $CaCO_3$ production from standing crop and turnover rate, and have turned to alkalinity depletion in the water column as a measure of community $CaCO_3$ production (for a review, see Smith, 1974).

Information about the organic carbon productivity of coral reefs is a more recent development. For the most part, present data are restricted to reef flats. The study by Odum and Odum (1955) at Enewetak Atoll* remains the most comprehensive description of reef-flat productivity. Estimates of organic carbon productivity in reef communities have relied primarily on oxygen changes as a measure of productivity. Kinsey and Domm (1974), Marsh (1974), and Smith (1974) have all reviewed the literature dealing with oxygen-derived estimates of organic carbon metabolism on coral reefs. In addition, Smith discussed the use of carbon dioxide to measure organic carbon metabolism in reef systems.

Other metabolites can also provide information on the organic carbon metabolism of aquatic communities. Studies of oxygen, carbon dioxide, phosphorus, and nitrogen flux across the windward reef flats of Enewetak Atoll demonstrate that there is no simple relationship between oxygen or carbon dioxide flux of coral reef communities and the instantaneous flux of other metabolites through these systems. Pilson and Betzer (1973) found no relationship between instantaneous oxygen metabolic rates and the uptake or release

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*This spelling of the atoll also known as "Eniwetok" has been officially sanctioned by the US Board of Geographic Names.

of phosphate. In fact, those authors could detect little or no instantaneous phosphate uptake or release in the Enewetak communities studied. Webb and his associates (1975) found nitrogen flux of the Enewetak reef-flat community to be even more complicated. The reef flat community exported all forms of dissolved nitrogen and apparently balanced this export with massive fixation of atmospheric nitrogen.

The above studies were undertaken in reef-flat environments where the residence time of water is only a few minutes. Such short-term incubations may not provide the most suitable conditions for quantifying and comparing the net biogeochemical fluxes of various materials. Advective flux may be so great that it masks biogeochemical changes. Moreover, short-term departures of biogeochemical fluxes from a mass balance among the materials in the system may obscure relationships among components even though such imbalances cannot be maintained indefinitely. The long-term net import, export, and storage of organic carbon must be proportional to the net flux and storage of nutrients.

In contrast with rapidly flushed reef flats, atoll lagoons retain water for relatively long timespans (von Arx, 1954). Thus lagoons can provide long-term, integrated records of community biogeochemical activity (Smith and Pesret, 1974). It is the purpose of the present study to consider an atoll lagoon in order to ascertain the net biogeochemical activity of a major, but largely unstudied, portion of coral reefs, and to compare the net rates of uptake or release for various biologically active materials within that lagoon. Circulation of water in an entire lagoon is more complex than water flow across a feef flat, so considerable attention is given in this paper to the manner in which the lagoon system has been analyzed. Budgets of material flux through the lagoon provide quantitative bases for comparing the various materials examined. The spatial distribution of biogeochemical fluxes can be compared with oceanographic, biotic, and physiographic patterns in the lagoon.

DESIGN OF SYSTEM ANALYSIS

Experience at Fanning Atoll, an atoll physiographically similar to Canton, but with certain pronounced differences, has been useful in designing the Canton study and in interpreting the results (see Smith and Pesret, 1974). The lagoons of both atolls are nearly landlocked. Fanning lagoon exchanges water with the open ocean through one large pass and two smaller ones, while Canton lagoon water exchanges at a single large pass with channels to either side of a small, artificial islet. As a result, the lagoon circulation at Canton is simpler than that at Fanning. Fanning has tidal flows at each of three passes, with net advection from east to west across the lagoon (Gallagher *et al.*, 1971). Tidal inflow and outflow at the single pass of Canton necessarily balance one another, except for a slight net inflow to offset evaporative loss.

Smith and Pesret (1974) calculated salt and water budgets for the Fanning lagoon to ascertain the relationship between the residence time (T) of water in the lagoon and salinity:

$$\mathrm{T\ (days)} = \frac{Z}{r}\left[\frac{S_o - S_l}{S_o}\right] \tag{1}$$

where Z is the mean lagoon water depth; r is the mean daily rainfall rate during and immediately preceding the salinity measurements; and S_o and S_l are the mean ocean and lagoon salinities, respectively. Smith and Pesret concluded that during the survey of Fanning lagoon the lagoon-wide effects of evaporation and groundwater seepage were small and approximately compensating processes in the water budget. These processes could be ignored in interpreting the lagoon-wide water budgets at Fanning, although there was a distinct groundwater effect around the lagoon margin.

Canton is ordinarily a dry island (Taylor, 1973). Consequently, details of the Canton water-budget model differ from those of Fanning. The evaporation rate (e) can no longer be ignored, but groundwater apparently can be. There is substantial groundwater at Canton (Guinther, this report), but there is no evidence of significant seepage from the groundwater into the lagoon (samples gathered by E. C. Evans III and E. B. Guinther). In fact, evaporation is a dominant term in the water budget at Canton, as evidenced by the elevated lagoon salinity first reported by van Zwaluwenburg (1941). The appropriate equation to describe lagoon-water residence time in this high-evaporation regime becomes:

$$\mathrm{T\ (days)} = \frac{Z}{(r-e)}\left[\frac{S_o - S_l}{S_o}\right] \tag{2}$$

Note that this general approach to calculating residence time is appropriate only if there is a salinity differential between the ocean and the lagoon. Without such a differential, the equation becomes indeterminant, because the denominator and numerator of the equations are then zero.

In the absence of a groundwater-induced low salinity rim around the lagoon margin, Eq. 2 also describes the relationship between local variations in salinity and the age of water at that locality (if one assumes constant water depth, rainfall, and evaporation throughout the lagoon). In that treatment of Eq. 2, S_l is the salinity at that locality, and T is a local estimate of residence time.

This salinity-residence time equation may be extended to calculate biogeochemical flux of materials within the lagoon. That is, for any constituent of seawater, there is a concentration change which may be called conservative and directly attributed to net evaporation or dilution (that is a "conservative change"); and there may be a residual ("nonconservative") change which results from biogeochemical uptake or release within the lagoon. For any material Y, the biogeochemical change with respect to salinity ($\triangle Y/\triangle S$) may be stated:

$$\frac{\triangle Y}{\triangle S}\ (\text{mole m}^{-3}\ \text{o/oo}^{-1}) = \left[\left(\frac{Y_o}{S_o}\right) S_l - Y_l\right] \Big/ (S_l - S_o) \qquad (3)$$

The subscripts o and l denote ocean and lagoon values, respectively. Both Y_o and Y_l are calculated according to regression equations relating Y to S. A positive value for $\triangle Y/\triangle S$ denotes net uptake from the water; negative is release. It follows from Eq. 2 and 3 that the change in Y with respect to the residence time of the water may also be calculated:

$$\frac{\triangle Y}{\mathrm{T}}\ (\text{mole m}^{-3}\ \text{day}^{-1}) = \frac{(r-e)\, S_o}{Z(S_l - S_o)} \left[\left(\frac{Y_o}{S_o}\right) S_l - Y_l\right] \qquad (4)$$

Multiplying Eq. 4 by the mean water depth expresses the rate of change in Y per unit map area:

$$\frac{\triangle Y}{\mathrm{T}}\ (\text{mole m}^{-2}\ \text{day}^{-1}) = \frac{(r-e)\, S_o}{S_l - S_o} \left[\left(\frac{Y_o}{S_o}\right) S_l - Y_l\right] \qquad (5)$$

Equation 5 and the appropriate regression equation for Y will be used to calculate the rate of change for each of several materials in the lagoon in response to biogeochemical processes for the Canton lagoon.

This record of $\triangle Y/\mathrm{T}$ provides an estimate of the net rate of biogeochemical change in Y as integrated from the pass to the S_l value in question. Equation 5 could be differentiated to yield an estimate of the biogeochemical rate $\triangle Y/\mathrm{T}$ at any location (or salinity). Because the simple polynomial equations impose obviously simplified patterns of change on the data (for example, a constant rate of change in uptake or release if the regression equation used is quadratic), that detailed information has not been extracted. The solution of Eq. 5 along with each appropriate regression equation for the Y_o's at progressively higher salinities provides an estimate of the cumulative history of water incubation between the pass and each salinity (or location) in question.

ANALYTICAL METHODS

Water sampling locations during November–December 1973 are shown in Fig. 7, and the parameters measured are listed in Table 1. In addition to the 1973 measurements, data are available from a preliminary survey conducted by Jokiel during June 1972. The 1972 data will be presented only in comparison with the more extensive 1973 data. Not all of the parameters are

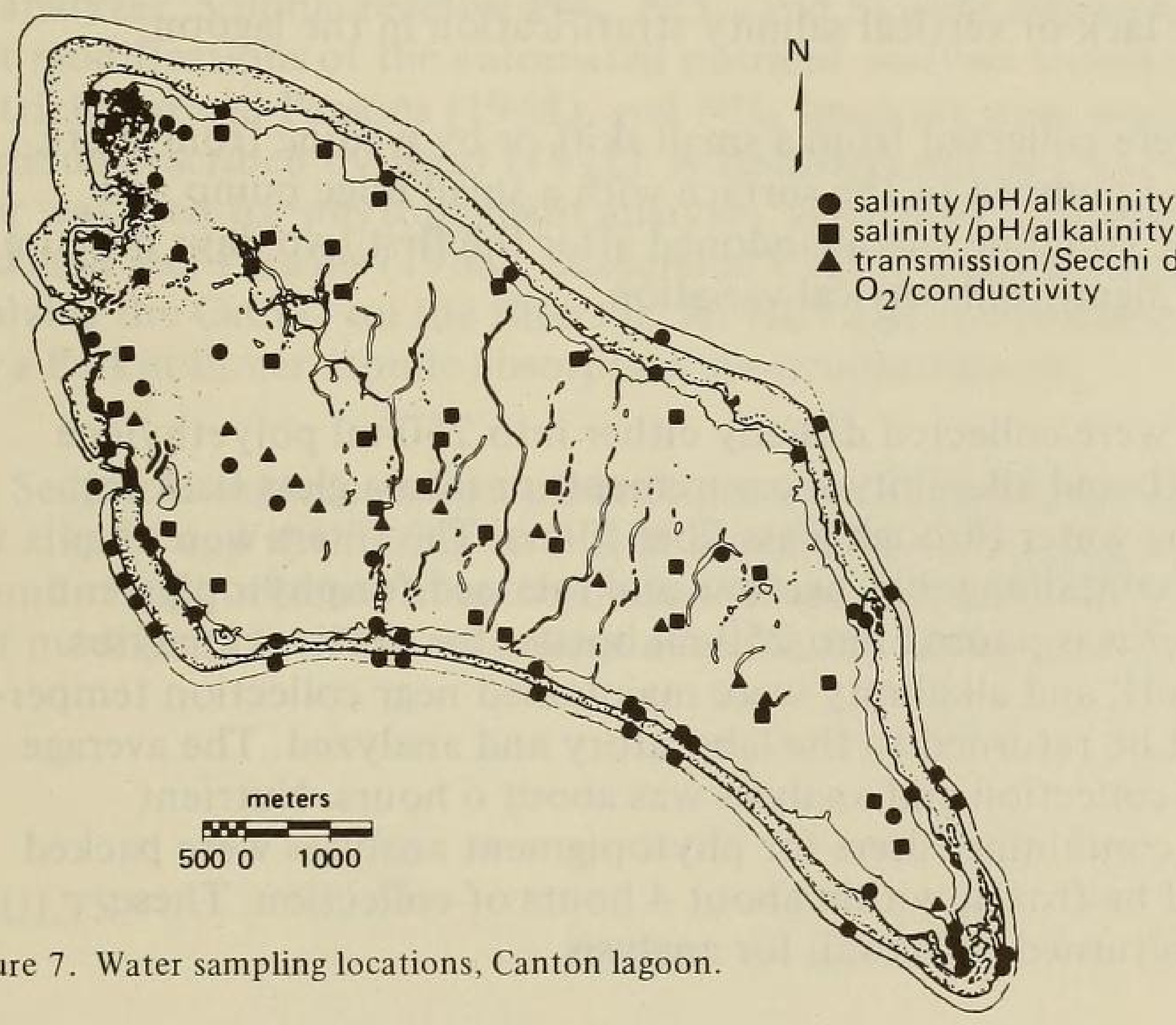

Figure 7. Water sampling locations, Canton lagoon.

Table 1. Water and sediment parameters measured in the Canton lagoon during the 1972 and 1973 surveys.

Parameter	1972	1973
Temperature	X	X
Salinity		X
Nutrients		X
pH		X
Alkalinity		X
O_2	X	X
Conductivity	X	X
Suspended $CaCO_3$		X
Suspended phytopigments		X
Secchi disc	X	X
% light transmission		X
Sediment organic carbon		X
Sediment mineralogy		X
Sediment grain size		X

considered in detail. For example, 0_2 measurements made with field polarographic cells yielded values consistently in near equilibrium with the atmosphere. These data warrant no further discussion. The lagoon was nearly isothermal, except for the marked phenomenon of marginal heating in the shallow waters around the lagoon rim. It is of interest to note that in 1972 the lagoon temperature was uniformly about 29°C, and during the 1973 survey the temperature was 27°C. Both values are within the range reported for monthly water temperatures at Canton (U. S. Coast and Geodetic Survey Publication 31-3, revised). Field values of water conductivity are of little value to this study except to confirm the lack of vertical salinity stratification in the lagoon.

Water samples were collected from a small skiff or by wading from shore. Midwater samples were pumped to the surface with a small bilge pump and garden hose. Midwater sampling was abandoned after the first two days because no parameter showed significant vertical variation.

Surface samples were collected directly either into 250-ml polyethylene bottles for salinity, pH, and alkalinity measurements or into a glass flask for on-site filtration of the water through glass fiber filters. The filters were then put into opaque vials containing 90% acetone and retained for phytopigment analyses; filtered water was poured into 250-ml bottles for nutrient analyses. Samples for salinity, pH, and alkalinity were maintained near collection temperature until they could be returned to the laboratory and analyzed. The average time between sample collection and analysis was about 6 hours. Nutrient samples and the vials containing filters for phytopigment analyses were packed in ice until they could be frozen within about 4 hours of collection. These frozen samples were returned to Hawaii for analysis.

At 13 stations, simultaneous measurements were made of Secchi disc readings and percent light transmission, and samples were taken for phytopigments and suspended $CaCO_3$. Secchi disc readings followed conventional field measurement procedures. Percent light transmission was measured with a Hydro-Products model 612 transmissometer equipped with a l-m measurement cell. Samples for phytopigment analyses were collected as described above; samples for $CaCO_3$ analyses were filtered onto 0.8μ pore-size Millipore filters, rinsed with deionized water, and then air-dried.

The laboratory used for salinity analyses was an air-conditioned room maintained near 25°C. A Plessey model 6230N laboratory conductivity salinometer was used for the analyses; it was standardized against a Copenhagen Water primary standard and working substandards. The laboratory used for pH and alkalinity measurements was not air-conditioned but was used because of its ample sink and working space. The room remained near 30°C during most of the measurement periods. A Corning model 101 pH meter and a combination electrode were used for all pH and alkalinity measurements. The analytical procedure closely followed that given by Smith and Pesret (1974). A computer program for calculating CO_2 parameters from pH, alkalinity, salinity, and temperature has been developed by Smith and is on file with the Hawaii Coastal Zone Data Bank (University of Hawaii).

Nutrient samples were returned to Hawaii and analyzed with a Technicon autoanalyzer. Soluble reactive PO_4, NO_3, and Si were measured according to slight modifications of the automated nutrient analysis techniques described by Strickland and Parsons (1968), and NH_3 analyses were modified from the technique described by Head (1971). A Beckman model DBG spectrophotometer was used for phytopigment analyses, after the technique described by Strickland and Parsons (1968). Suspended $CaCO_3$ analyses were performed by dissolving the $CaCO_3$ on the filters in 3N HCl and then measuring Ca and Mg with a Perkin Elmer atomic absorption spectrophotometer.

Sediment organic carbon percentages were determined by weighing a sediment aliquot and then using an F & M model 185 CHN analyzer to measure the amount of CO_2 released at an oxidation temperature of 700°C, according to a slight modification of the technique described by Telek and Marshall (1974).

RESULTS

Salt and Water Budgets

Equation 2 is used to construct the salt and water budgets of the lagoon.

The mean lagoon depth was determined by gridding the Hydrographic Office Chart of the Canton Island Lagoon (No. 83105) into approximately 2,200 squares and estimating the mean depth at each grid intersection. The mean lagoon depth was found to be 6.2 m.

Rainfall records have been maintained at one or both of two weather stations at Canton Atoll since 1940, except for three interruptions (1941–1942, 1945, 1967–1971). Taylor (1973) reports the available data from these two stations through 1972 (except for the period from December 1971 through May 1972; records from that period, plus the period from January 1973 through October 1974, were obtained from U. S. Air Force records). Table 2 summarizes relevant aspects of the rainfall data.

Of particular interest to the present investigation is the period from April 1973 through March 1974. The rainfall averaged about 0.6 mm/day during that period, with only the month of August differing significantly from that average. This average is less than one-third the long-term mean daily rainfall. By contrast, the average rainfall from April 1972 through March 1973 was about 8 mm/day, or four times the long-term mean. Thus over the course of 2 years, Canton experienced the wettest and one of the driest periods in its recorded history.

Evaporation-rate data comparable to these extensive rainfall records are not available, but it is possible to estimate evaporation during and immediately preceding this survey.

Evaporation was measured in plastic containers filled with seawater, then shaded from the sun but exposed to the wind. Measurements were made both in 12-cm-deep pans monitored hourly for periods of up to 9 hours and in a 50-cm-deep container monitored twice daily for 9 days. The parameters measured were initial water depth in the container and salinity at each time increment. Evaporation can be determined more precisely from a change in salinity than from direct depth measurements. Evaporation-pan procedures are generally open to question, largely because of differences between water temperatures in the evaporation pan and the temperature of the water body of interest

Table 2. Canton Atoll rainfall.

Month	1937-1974 mean		1971		1972		1973		1974	
	mm	mm/day	mm	mm/day	mm	mm/day	mm	mm/day	mm	mm/day
January	88.9	(2.9)	–	–	17.8	(0.6)	526.3	(17.0)	0.0	(0.0)
February	45.8	(1.6)	–	–	13.5	(0.5)	286.8	(10.2)	2.3	(0.1)
March	58.5	(1.9)	–	–	16.3	(0.5)	235.2	(7.6)	16.8	(0.5)
April	90.1	(3.0)	–	–	154.2	(5.1)	34.0	(1.1)	69.3	(2.3)
May	76.1	(2.5)	–	–	84.8	(2.7)	33.5	(1.1)	53.6	(1.7)
June	60.4	(2.0)	–	–	21.9	(0.7)	8.6	(0.3)	58.7	(1.9)
July	61.2	(2.0)	–	–	199.6	(6,4)	22.9	(0.7)	100.8	(3.3)
August	56.7	(1.8)	–	–	78.2	(2.5)	82.8	(2.7)	27.9	(0.9)
September	33.0	(1.1)	–	–	134.4	(4.5)	20.1	(0.7)	19.8	(0.7)
October	35.2	(1.1)	–	–	428.5	(13.8)	5.1	(0.2)	5.3	(0.2)
November	51.7	(1.7)	–	–	312.9	(10.4)	0.3	(0.0)	–	–
December	69.3	(2.2)	1.5	(0.1)	427.2	(13.8)	5.1	(0.2)	–	–
Total	726.9	(2.0)	–	–	1889.3	(5.2)	1260.6	(3.5)	–	–

NOTE:

		mm	mm/day
wettest 12-month period:	April 1972–March 1973	2890.0	(7.9)
one of driest 12-month periods:	April 1973–March 1974	231.5	(0.6)
driest 12-month period:	January 1954–December 1954	196.1	(0.5)

(in this case, the lagoon). However, the difference between the pan and lagoon water temperatures never exceeded 1°C, except for elevated temperatures found locally on the shallow intertidal flats fringing the lagoon. Three experiments in the shallow pans and one in the deep container all yielded evaporation rates between 8 and 9 mm/day.

Jacobs (1942) gives a formula for calculating evaporation rate (e) from wind velocity (w) at some height, water vapor pressure at that height (p_h), and the vapor pressure at the sea surface (p_o):

$$e \text{ (mm/day)} = 0.14\,(p_o - p_h)\,w \tag{6}$$

The mean wind velocity during the survey, as averaged from U. S. Air Force records, was 6 m/s; mean air temperature and water temperature were both 27°C; mean relative humidity, as calculated from temperature and dew point, was 72%. From Sverdrup *et al.* (1942), the vapor pressure at that temperature and humidity can be calculated to be 25 mbar. At 100% humidity (the assumed sea-surface value) the vapor pressure is about 35 mbar. The calculated evaporation rate is 8 mm/day, the same as the measured values. This lagoon evaporation rate is about twice the long-term mean value reported by Wyrtki (1966) for the open ocean in the vicinity of Canton.

Figure 8 is a map of salinity distribution in the lagoon in December 1973. There was no vertical stratification, so available surface and midwater data have

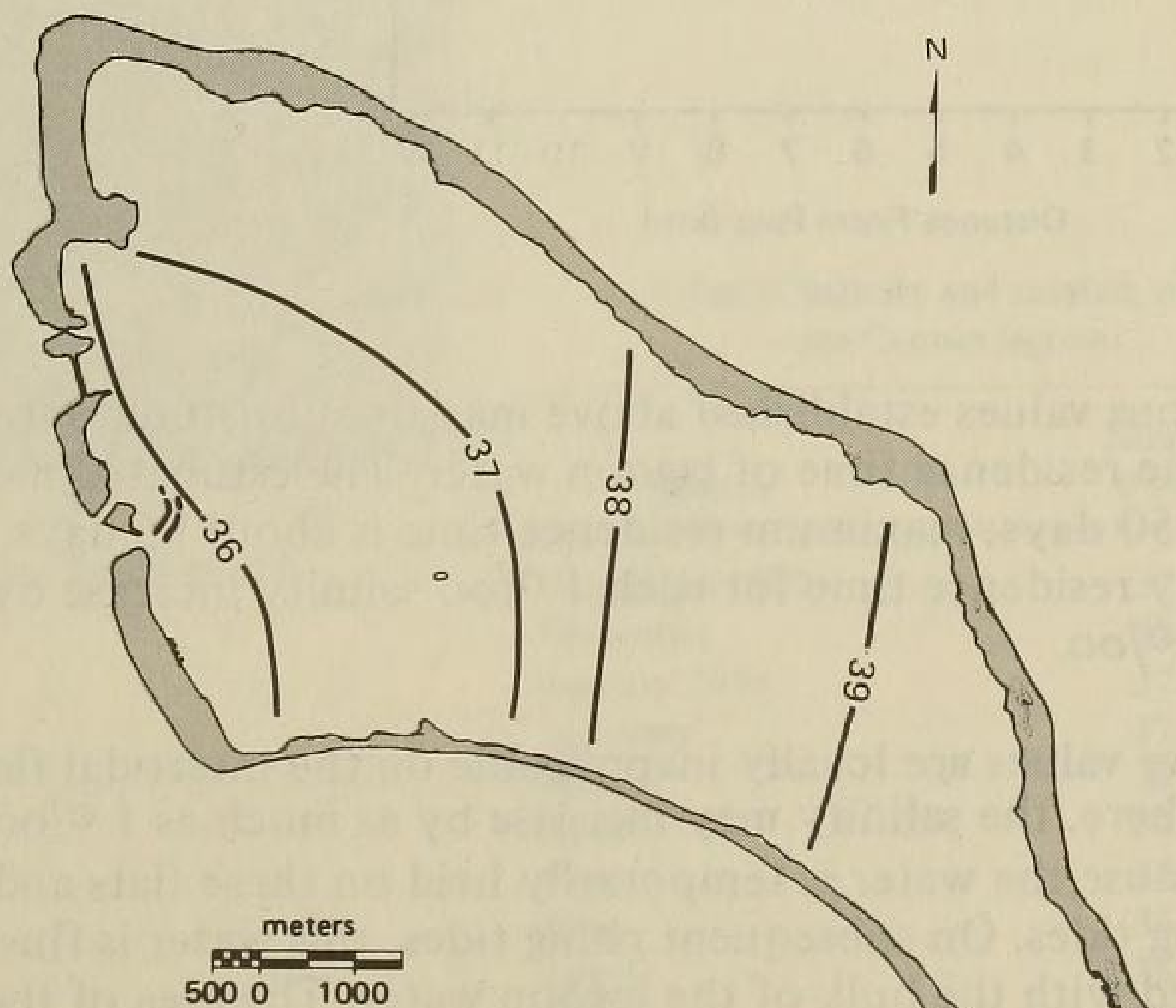

Figure 8. Salinity isopleths (°/oo) in the Canton lagoon.

been combined into this single map. Figure 9 shows salinity as a function of distance from the lagoon pass. At the time of the survey, salinity increased with distance from the pass from an oceanic value of 35.7 $^o/oo$ to a back-lagoon value of about 39.5 $^o/oo$. The trend is well approximated (coefficient of determination = 96%) by the following empirical quadratic regression equation:

$$S_l\ (^o/oo) = 35.53 + 0.563X - 0.0202X^2 \qquad (7)$$

S_l is the calculated salinity at any location X km from the pass. Planimetry of the salinity map (Fig. 9) yields a mean lagoon salinity of about 37.7 $^o/oo$.

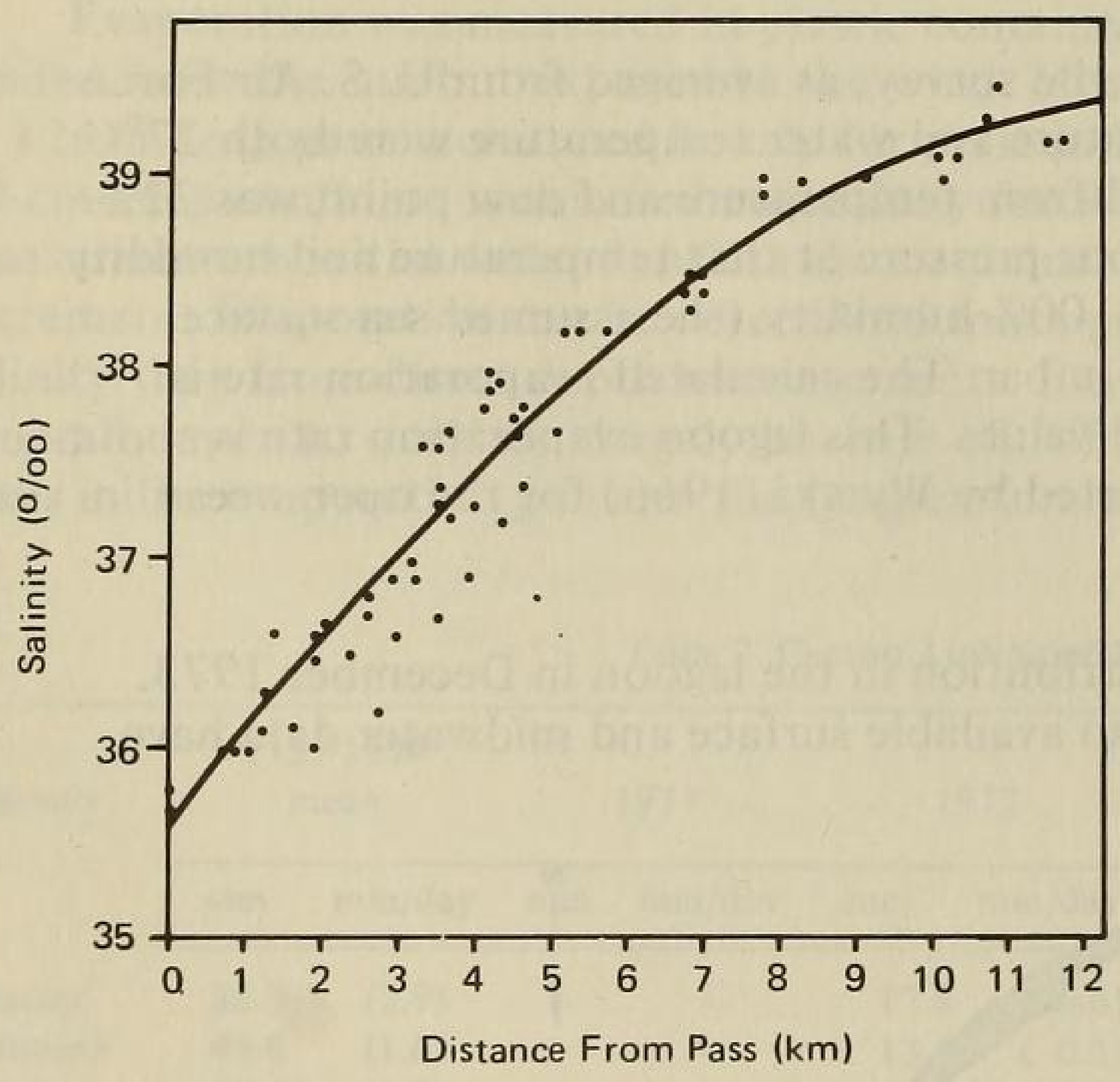

Figure 9. Salinity versus distance from pass, including quadratic regression line.

The various values established above may be substituted into Eq. 2 in order to calculate the residence time of lagoon water. The estimated mean residence time is about 50 days; maximum residence time is about 95 days, and there is about a 25-day residence time for each 1 $^o/oo$ salinity increase over the oceanic value of 35.7 $^o/oo$.

The above values are locally inapplicable on the intertidal flats along the lagoon rim. There, the salinity may increase by as much as 1 $^o/oo$ over a single tide cycle because the water is temporarily held on these flats and heated during daytime falling tides. On subsequent rising tides, this water is flushed off the flats and mixed with the bulk of the lagoon water. The area of these intertidal flats is sufficiently small so that this local effect has been ignored in constructing lagoon-wide budgets.

Salinity data gathered by Jokiel during a trip to Canton in June 1972 and samples shipped to Hawaii by members of the U. S. Air Force after the 1973 survey establish temporal variations in the patterns described above. The 19 samples gathered by Jokiel have been matched with samples collected from approximately the same locations during the present survey. Data are reported as "salinity excess" above oceanic values, because Jokiel's salinity probe was not adequately calibrated to establish absolute salinities. Figure 10 shows that the 1972 salinity excesses were generally somewhat lower than the 1973 values (which are also expressed here as salinity excesses). This pattern is to be expected, because rainfall during early 1972 was somewhat higher than rainfall during late 1973 (Table 2). Samples collected from the northern corner of the lagoon and shipped to Hawaii from November 1973 until October 1974 also showed a consistent pattern (Table 3). Salinity remained relatively constant

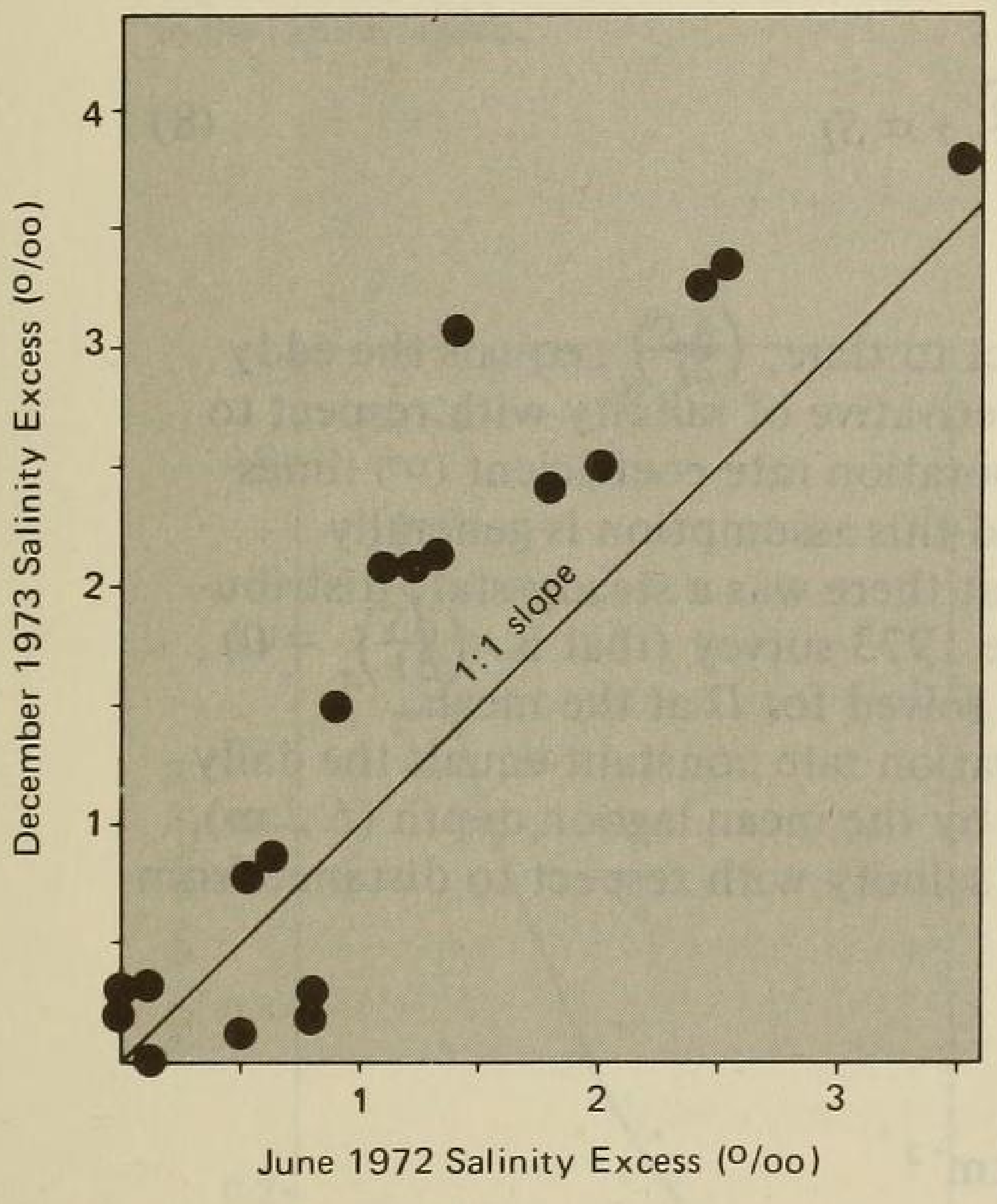

Figure 10. June 1972 versus December 1973 "salinity excess" above oceanic values.

Table 3. Salinity and rainfall, northern portion of the Canton lagoon.

Month	Salinity (°/oo)	Monthly rain (mm)
November 1973	37.8	0
December	37.8	5
January 1974	37.9	0
February	37.5	2
March	38.1	17
April	37.7	69
May	37.0	54
June	36.4	59
July	36.5	101
August	36.5	28
September	37.0	20
October	37.5	5

from November until April 1974 and then decreased by about 1 o/oo. Rainfall from April through July was markedly higher than rainfall over the previous months, so the salinity decrease is to be expected. From August through October, rainfall dropped and salinity rose.

This salinity differential between the ocean and lagoon is obviously maintained by a combination of evaporative water loss, replacement by a net inflow of ocean water, and dispersion of this ocean water through the lagoon. The volume of water entering the lagoon on each rising tide averages about 11% of the total lagoon volume (0.7 m average tidal range divided by 6.2 m average lagoon depth), so apparently only a small fraction of each tidal prism actually remains in the lagoon. Because the exchange of water between the ocean and lagoon is restricted to a single pass, a one-dimensional eddy diffusion model may be assumed to describe salt dispersion through the lagoon (A. Okubo, personal communication):

$$\left(\frac{\partial S}{\partial t}\right)_x \text{ (o/oo day}^{-1}) = \frac{D\partial^2 S}{\partial X^2} + \propto S_l \qquad (8)$$

The local change in salinity with respect to time, $\left(\frac{\partial S}{\partial t}\right)_x$, equals the eddy diffusion coefficient (D) times the second derivative of salinity with respect to distance from the pass (X) plus the net evaporation rate coefficient ($\propto$) times the local salinity (S_l). It can be assumed (and this assumption is generally supported by the data in Tables 2 and 3) that there was a steady-state distribution of salinity before and at the time of the 1973 survey (that is, $\left(\frac{\partial S}{\partial t}\right)_x = 0$). Equation 8 can therefore be rearranged and solved for D at the mean lagoon salinity (S_l = 37.7 o/oo). The evaporation rate constant equals the daily net evaporation rate (0.007 m/day) divided by the mean lagoon depth (6.2 m), or 0.00113 day^{-1}. The second derivative of salinity with respect to distance from the pass can be calculated from Eq. 7:

$$\frac{\partial^2 S}{\partial X^2} = 0.0404 \text{ o/oo km}^{-2}$$

Substituting these values into Eq. 8 yields D = 1.054 km^2/day, or 1.2 x 10^5 cm^2/s. This value corresponds closely to the value of 1.0 x 10^5 cm^2/s calculated from Okubo's (1971) equation relating D to eddy size (using 12 km, the distance from the pass to the back lagoon at Canton, as the appropriate eddy size). It therefore seems probable that the net dispersion of materials through the lagoon at Canton can be accounted for in terms of eddy diffusion.

Nutrient Budgets

Figure 11 is a map of phosphate distribution throughout the lagoon, and Fig. 12 is a plot of that nutrient against salinity. The PO_4 values decreased from a mean of about 0.6 mmole/m^3 near the pass to about 0.1 mmole/m^3 in the back lagoon.* This decrease is empirically well-described (coefficient of determination = 89%) by the following quadratic regression equation:

$$PO_4 \text{ (mmole/m}^3\text{)} = 82.567 - 4.289S + 0.0448S^2 \qquad (9)$$

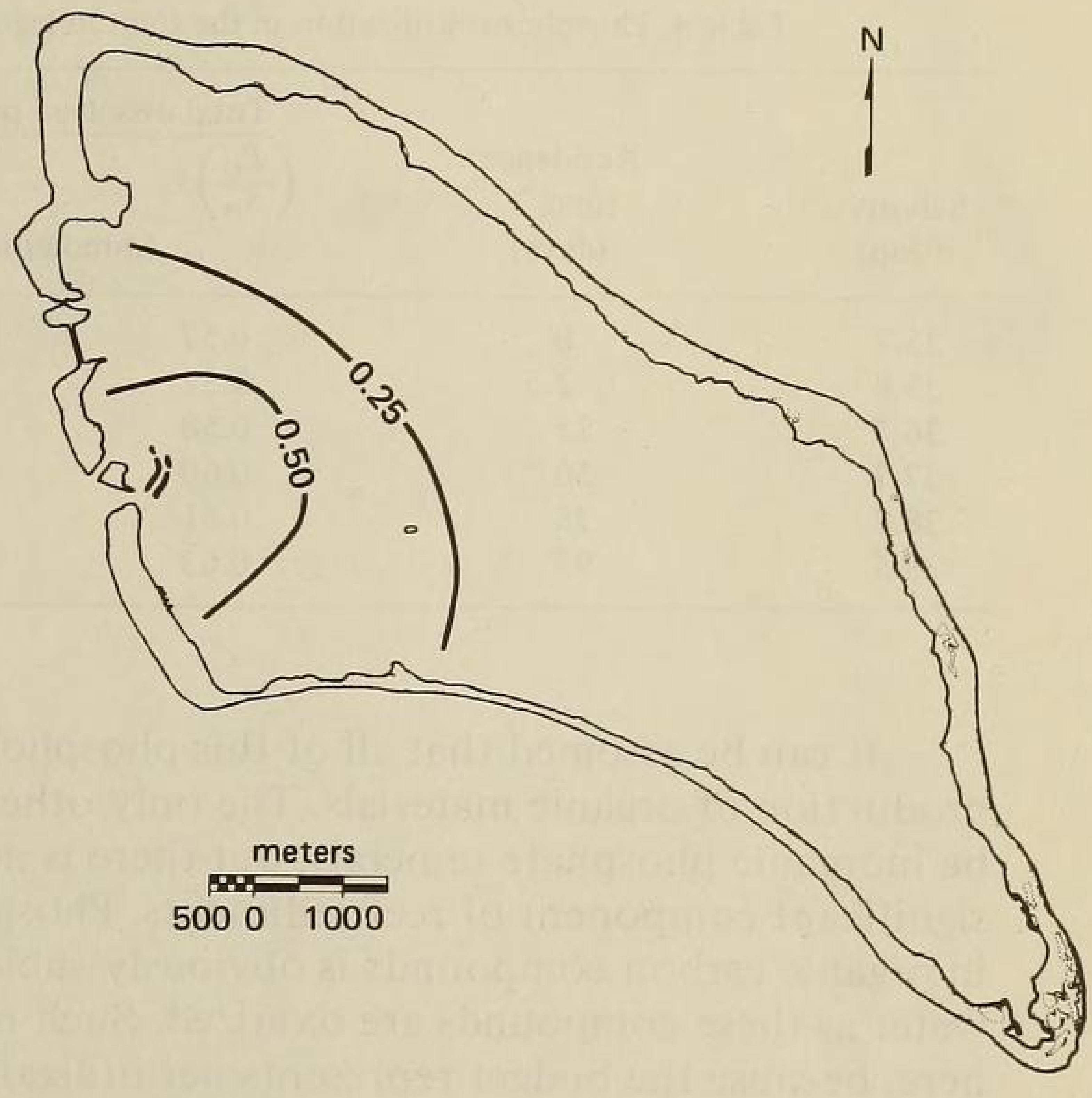

Figure 11. Phosphate isopleths (mmole/m^3) in the Canton lagoon.

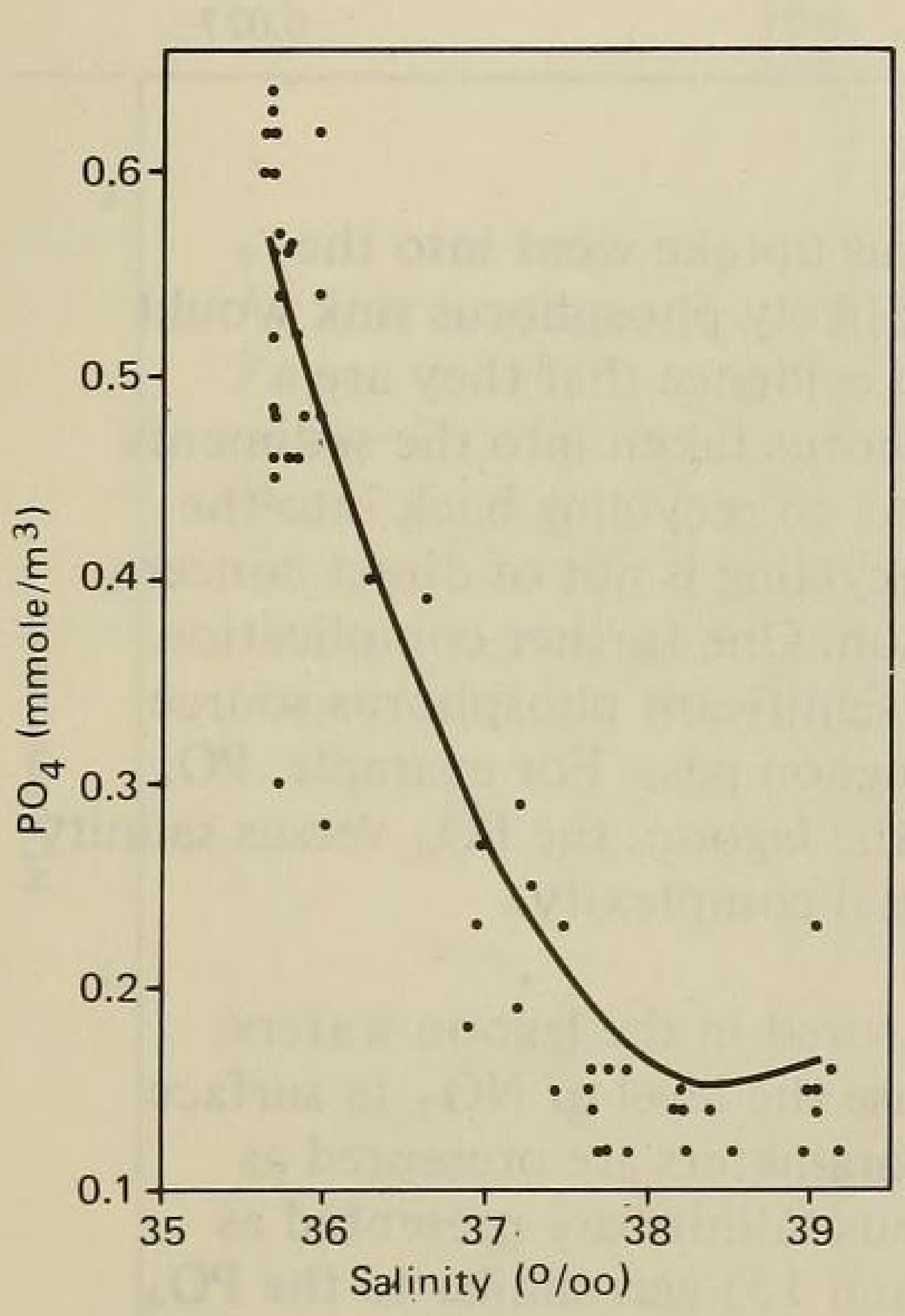

Figure 12. Phosphate versus salinity, including quadratic regression line.

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*For convenience, all notation of nutrient concentrations is given here in terms of mmole/m^3, instead of the more conventional–but equivalent–notation of μg-atom/liter.

Table 4 presents the rates of biogeochemical phosphorus flux as calculated from Eq. 5 and 9. The table presents the data for phosphorus change during the first 0.1 $^{o}/oo$ salinity increase, as indicative of rates near the pass. The changes are then reported for each unit salinity increase above oceanic (up to 38.7 $^{o}/oo$) and finally at 39.5 $^{o}/oo$ (nominally the maximum lagoon salinity). There was net phosphorus uptake throughout the lagoon, and the uptake rate decreased with increasing salinity. Near the pass, the uptake rate was 0.074 mmole m^{-2} day^{-1}; in the back lagoon the uptake rate was 0.027 mmole m^{-2} day^{-1}.

Table 4. Phosphorus utilization in the Canton lagoon, as calculated from Eq. 5 and 9.

Salinity ($^{o}/oo$)	Residence time, T (days)	Total dissolved phosphorus $\left(\frac{P_o}{S_o}\right)S_l$ (mmole/m^3)	P_l	Phosphorus utilization, $\frac{\Delta P}{T}$ (mmole $m^{-2}day^{-1}$)
35.7	0	0.57	0.57	–
35.8	2.5	0.57	0.54	0.074
36.7	25	0.58	0.32	0.065
37.7	50	0.60	0.18	0.052
38.7	75	0.61	0.15	0.038
39.5	95	0.63	0.21	0.027

It can be assumed that all of this phosphorus uptake went into the production of organic materials. The only other likely phosphorus sink would be inorganic phosphate minerals, but there is no evidence that they are a significant component of reef sediments. Phosphorus taken into the sediments in organic carbon compounds is obviously subject to recycling back into the water as these compounds are oxidized. Such recycling is not of direct concern here, because the budget represents net utilization. One further complication in the phosphorus budget is the possibility of a significant phosphorus source other than dissolved reactive PO_4 input at the lagoon pass. For example, PO_4 derived from phosphatic rocks might seep into the lagoon; the PO_4 versus salinity diagram (Fig. 12) does not suggest such additional complexity.

Two forms of dissolved nitrogen were measured in the lagoon waters: NO_3 and NH_3. Nitrite was not measured, because the level of NO_2 in surface seawater is ordinarily very low. Maps of these parameters are presented as Fig. 13 and 14, and plots of these materials versus salinity are presented as Fig. 15 and 16. The NO_3 distribution (Fig. 13 and 15) was similar to the PO_4 pattern; values decreased from levels of about 2.5 mmoles NO_3/m^3 near the pass to near 0 in the back lagoon. The NH_3 pattern was more complex. Values were about 1.5 mmoles NH_3/m^3 near the pass, followed by an abrupt decrease to about 0.4 mmole/m^3 throughout much of the lagoon. However, there were

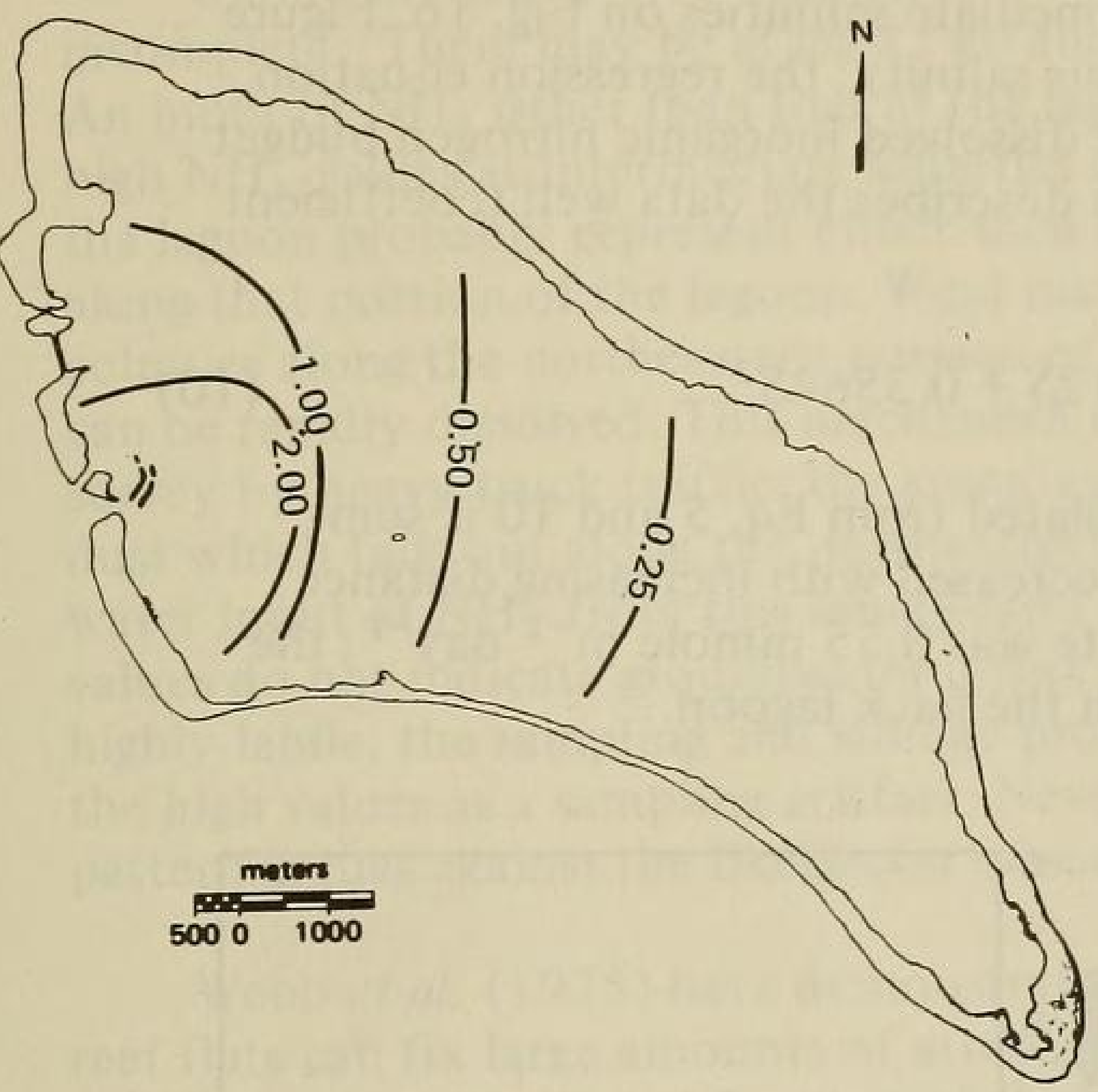

Figure 13. Nitrate isopleths (mmole/m^3) in the Canton lagoon.

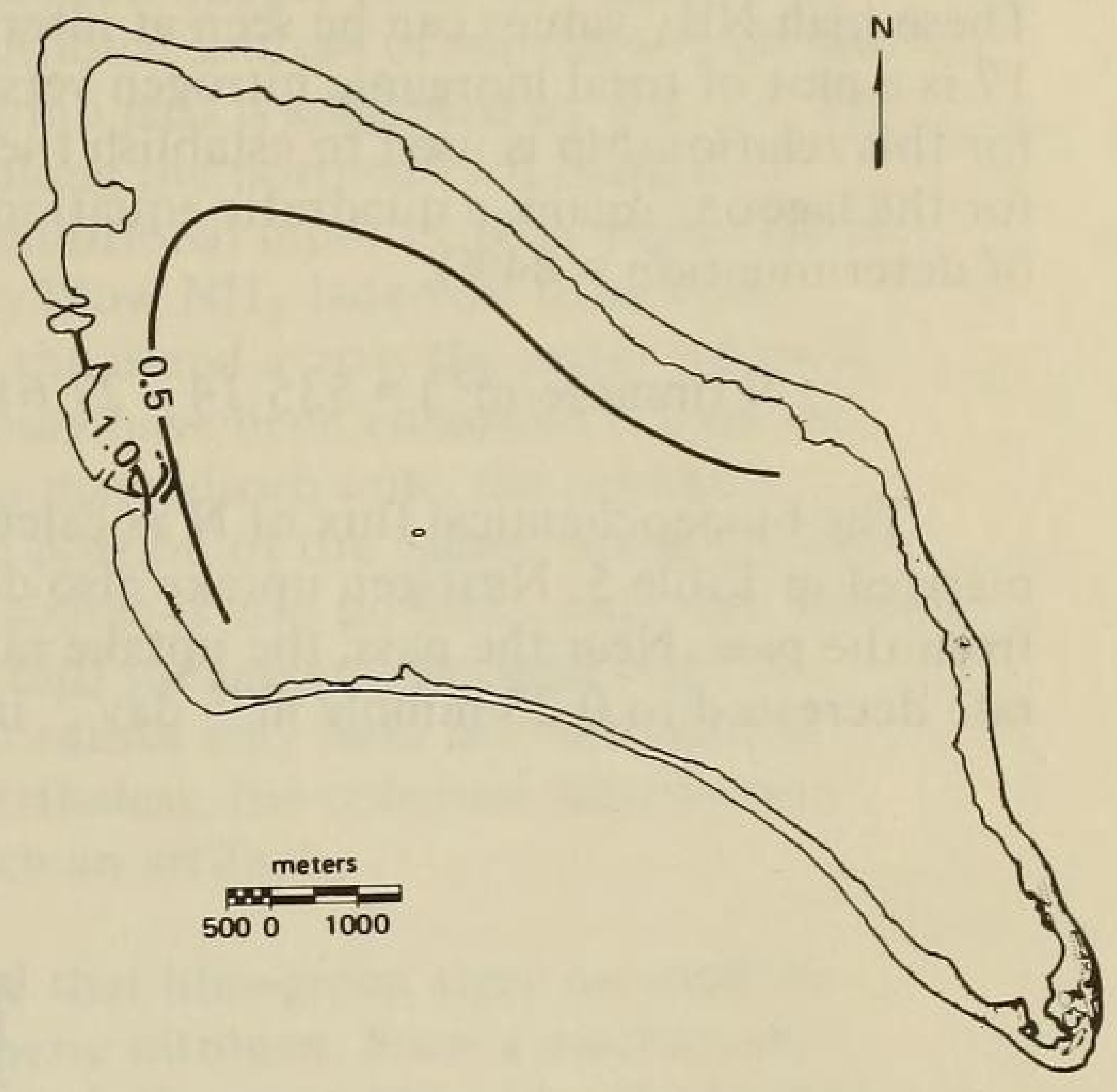

Figure 14. Ammonia isopleths (mmole/m^3) in the Canton lagoon.

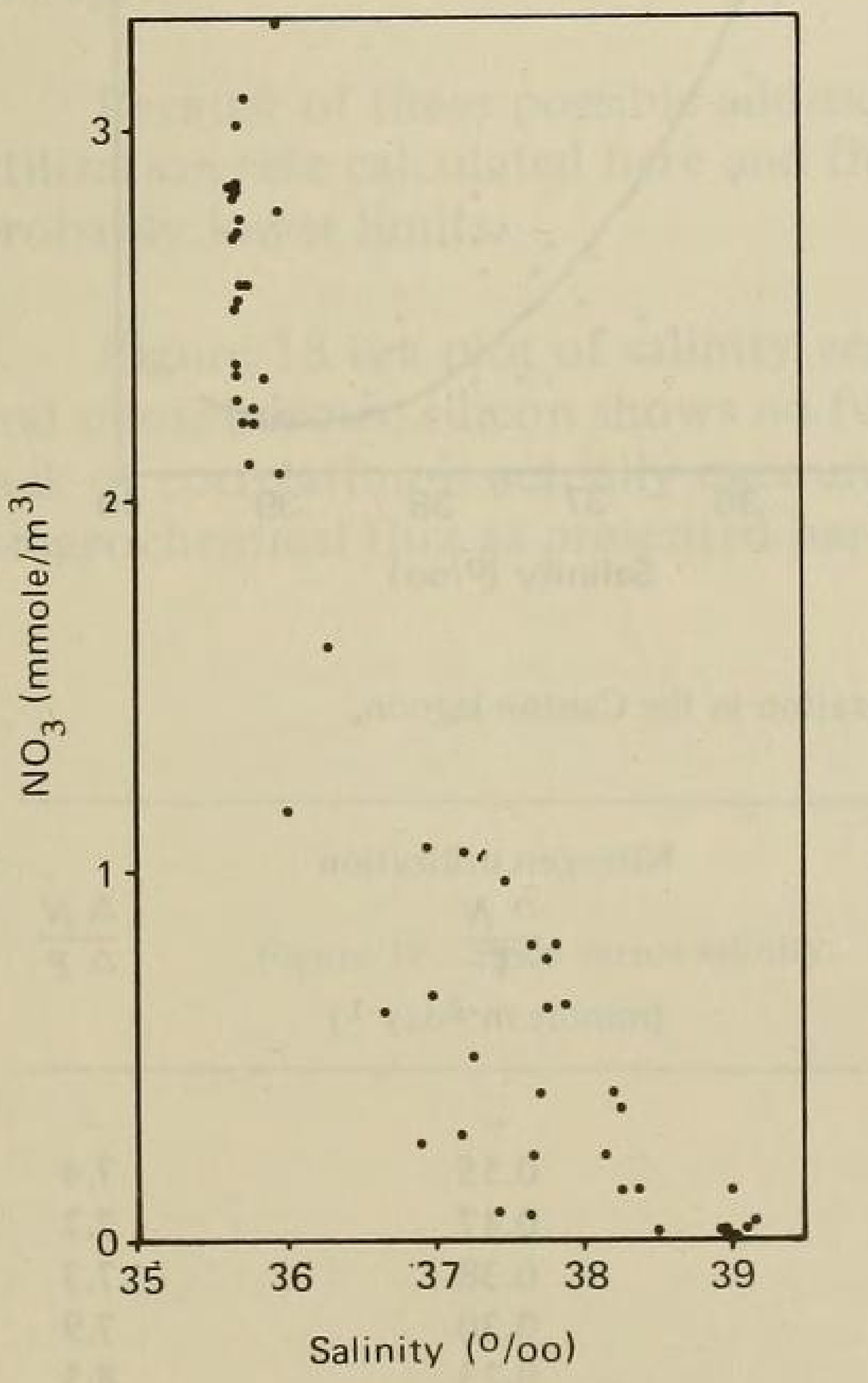

Figure 15. Nitrate versus salinity.

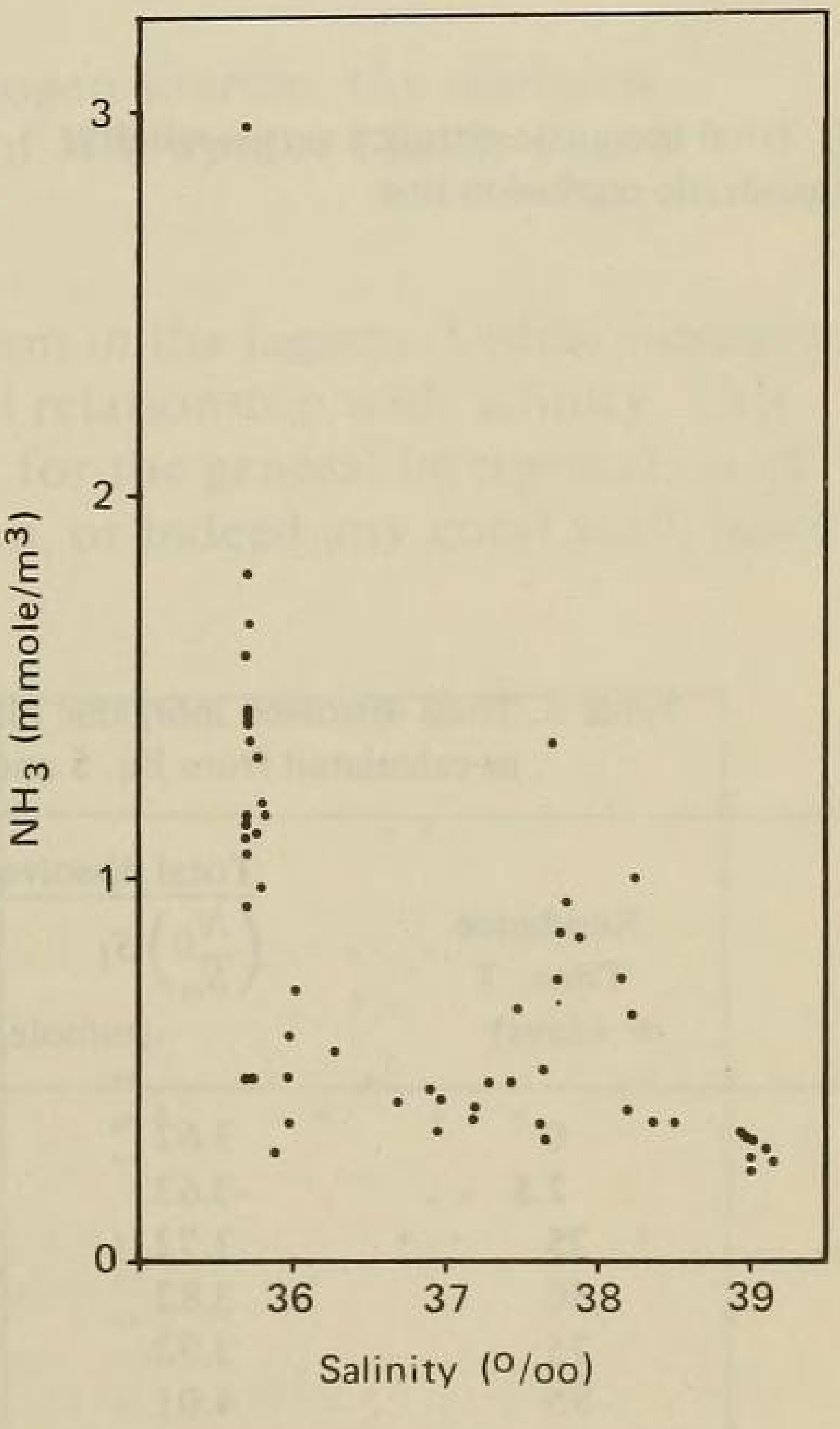

Figure 16. Ammonia versus salinity.

high values (near 1 mmole/m^3) along the northeastern margin of the lagoon. These high NH_3 values can be seen at intermediate salinities on Fig. 16. Figure 17 is a plot of total inorganic nitrogen versus salinity; the regression equation for this relationship is used to establish the dissolved inorganic nitrogen budget for the lagoon. Again, a quadratic equation describes the data well (coefficient of determination = 84%):

$$N\ (\text{mmole/m}^3) = 535.14 - 27.612S + 0.3564S^2 \tag{10}$$

The biogeochemical flux of N as calculated from Eq. 5 and 10 is summarized in Table 5. Nitrogen uptake also decreased with increasing distance from the pass. Near the pass, the uptake rate was 0.55 mmole m^{-2} day^{-1}; the rate decreased to 0.23 mmole m^{-2} day^{-1} in the back lagoon.

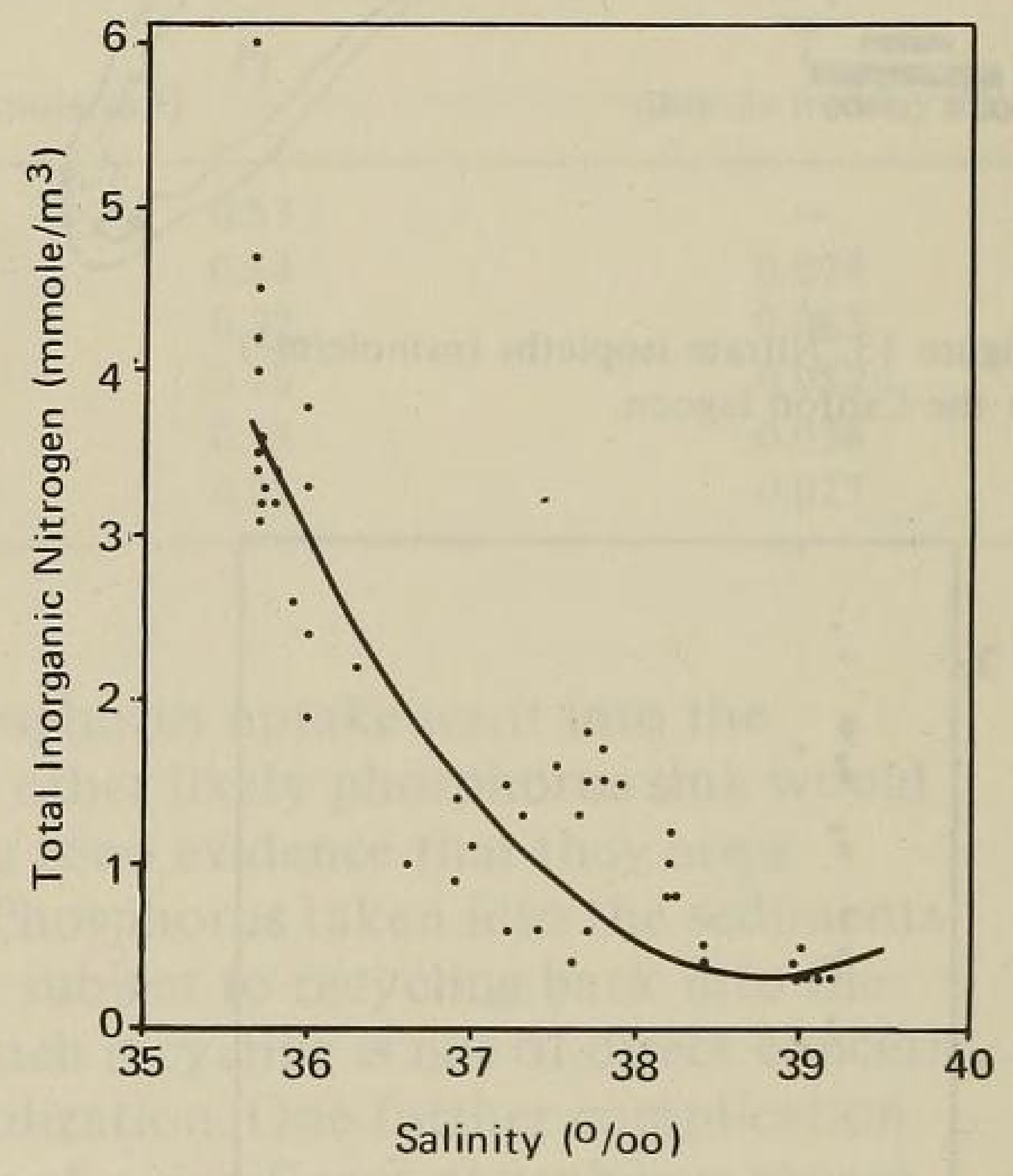

Figure 17. Total inorganic nitrogen versus salinity, including quadratic regression line.

Table 5. Total dissolved inorganic nitrogen utilization in the Canton lagoon, as calculated from Eq. 5 and 10.

Salinity (o/oo)	Residence Time, T (days)	Total dissolved nitrogen $\left(\frac{N_o}{S_o}\right) S_l$ (mmole/m^3)	Total dissolved nitrogen N_l (mmole/m^3)	Nitrogen utilization $\frac{\Delta N}{T}$ (mmole m^{-2}day^{-1})	$\frac{\Delta N}{\Delta P}$
35.7	0	3.62	3.62	–	–
35.8	2.5	3.63	3.41	0.55	7.4
36.7	25	3.72	1.81	0.47	7.2
37.7	50	3.82	0.72	0.38	7.3
38.7	75	3.92	0.33	0.30	7.9
39.5	95	4.01	0.54	0.23	8.5

Unlike the phosphorus budget, the nitrogen budget must be regarded as incomplete. There may be at least two additional sources of nitrogen in the lagoon. An input of NH_3 other than that at the lagoon pass is suggested by Fig. 14. The high NH_3 values at intermediate salinities along the northeastern margin of the lagoon probably represent either such additional input or NH_3 regeneration along that portion of the lagoon. Wind may blow NH_3-laden air from bird colonies along the northeastern portion of the island across the water where it can be rapidly dissolved. This mechanism may have been enhanced during the survey by heavy truck traffic; the ammonia may adsorb onto the resultant dust which falls out along the northeastern portion of the island. Some groundwater input of NH_3 from this same island source is also possible, although salinity values do not indicate groundwater influx into the lagoon. Because NH_3 is highly labile, the sampling and storage procedures may have also introduced the high values as a sampling artifact. Nevertheless, the coherent distribution pattern argues against the likelihood of such an artifact.

Webb *et al.* (1975) have demonstrated that blue-green algae on shallow reef flats can fix large amounts of atmospheric nitrogen. Such a mechanism could supply a significant fraction of the total nitrogen utilized by the Canton lagoon community. Drouet (in Degener and Degener, 1959) lists several genera of blue-green algae which are found at Canton and which are known to fix nitrogen.

Because of these possible additional nitrogen sources, the nitrogen utilization rate calculated here and the ratio of N:P uptake (Table 5) are probably lower limits.

Figure 18 is a plot of salinity versus silicon in the lagoon. Unlike nitrogen and phosphorous, silicon shows no functional relationship with salinity. This lack of correlation is actually encouragement for the general interpretation of biogeochemical flux as presented here. Canton, or indeed any coral atoll, has a

Figure 18. Silica versus salinity.

biotic community overwhelmingly dominated by calcification rather than silicification as the major form of net skeletogenesis; hence, any calculation suggesting significant net silicon uptake in a reef environment would be viewed with some surprise.

Carbon Dioxide Budget

Of the various budgets presented here, the carbon dioxide budget is perhaps the most complex. In addition to evaporative change in the CO_2 content of the seawater, there is also change due to organic carbon production or consumption, $CaCO_3$ precipitation or solution, and gas exchange across the air–sea interface.

Figures 19 and 20 are maps of two CO_2 parameters: total CO_2 and total alkalinity. Figures 21 and 22 are plots of these CO_2 parameters versus salinity.

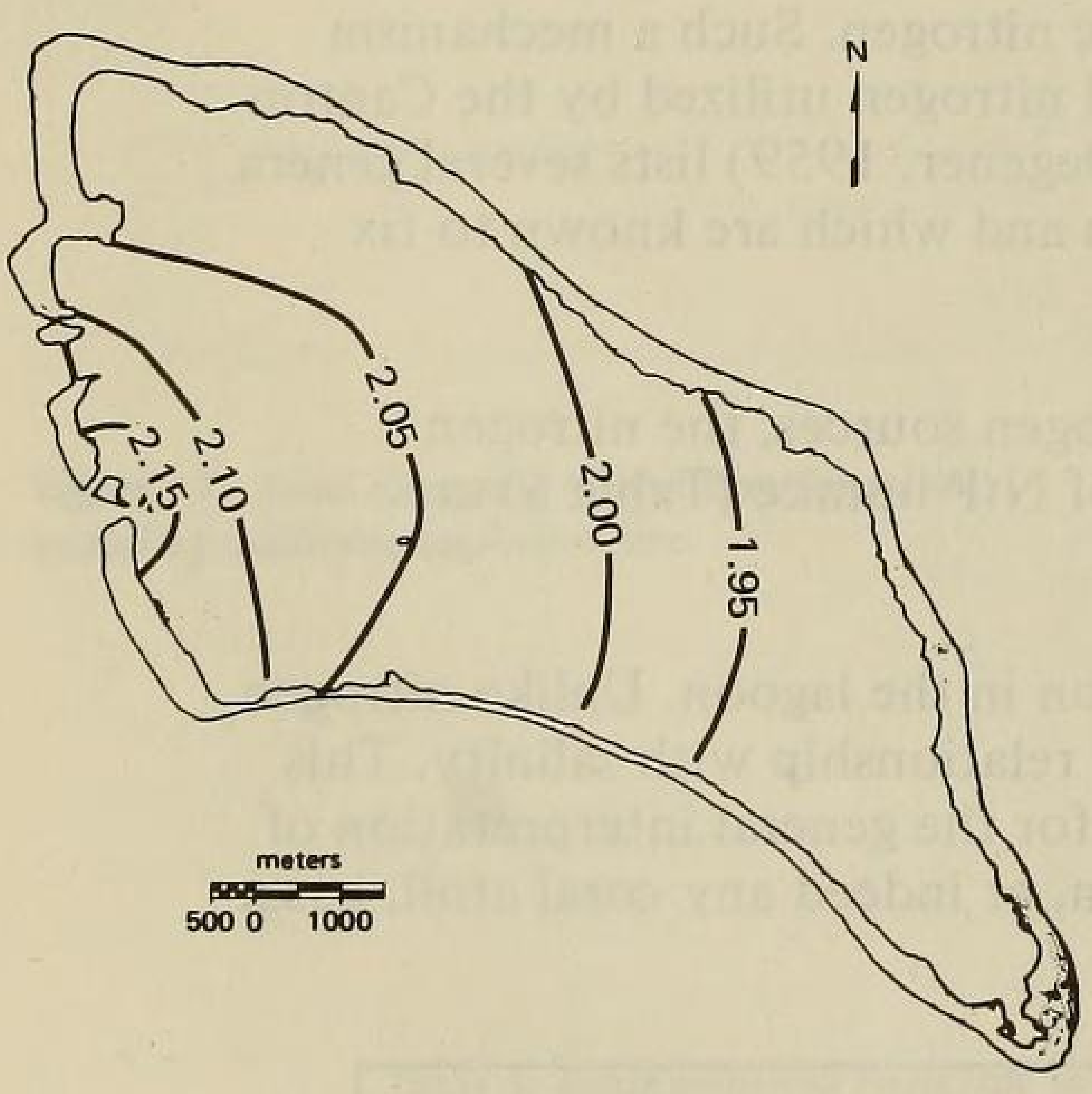

Figure 19. Total CO_2 isopleths (mole/m^3) in the Canton lagoon.

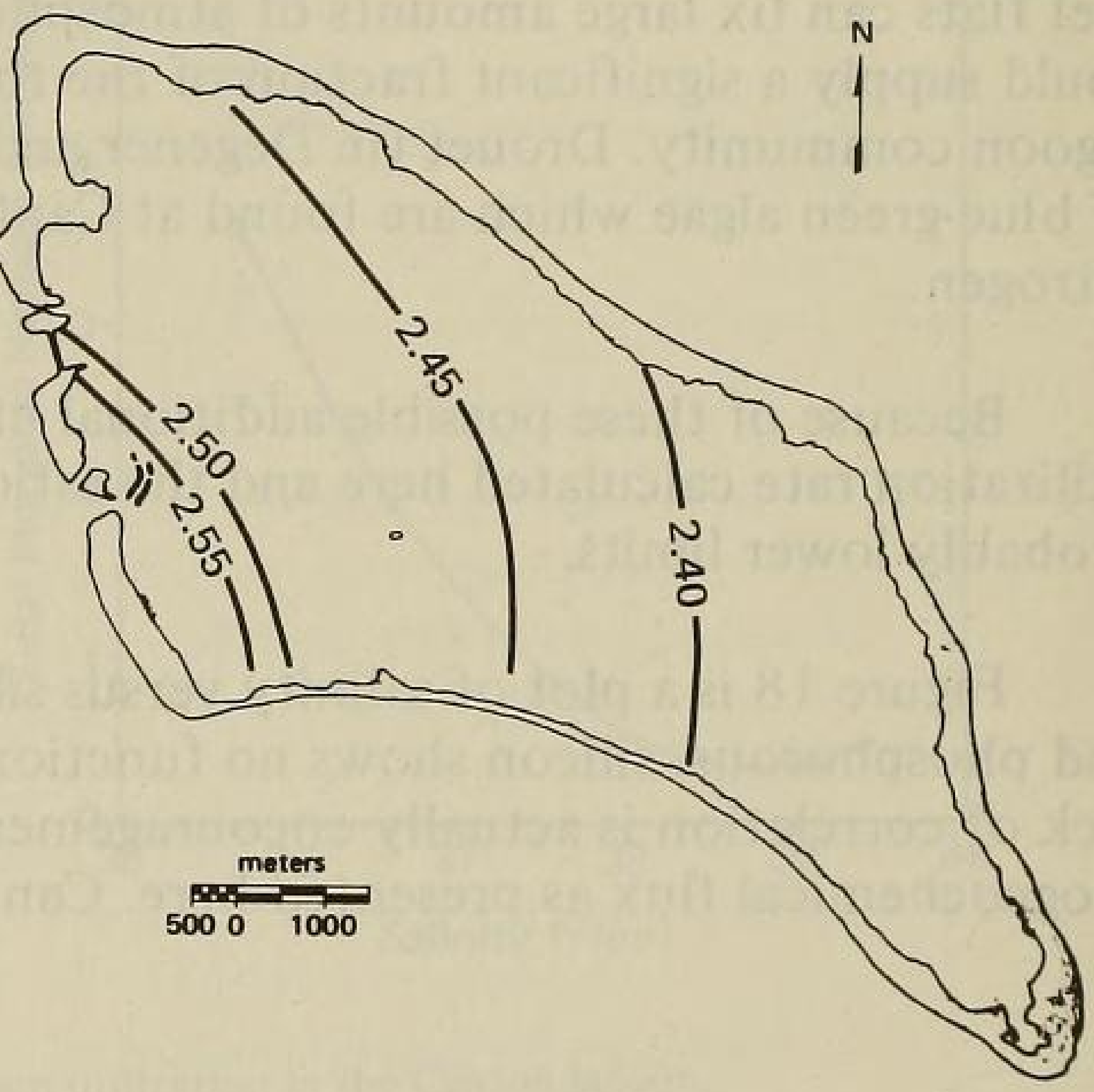

Figure 20. Total alkalinity isopleths (equiv/m^3) in the Canton lagoon.

Total CO_2 decreased regularly from about 2.2 moles/m^3 near the pass to about 1.9 moles/m^3 in the back lagoon. The decrease with respect to salinity is well-approximated (coefficient of determination = 80%) by a linear regression equation:

$$CO_2\ (\text{mole/m}^3) = 4.156 - 0.0568S \qquad (11)$$

Higher-order regression equations do not improve this fit significantly.

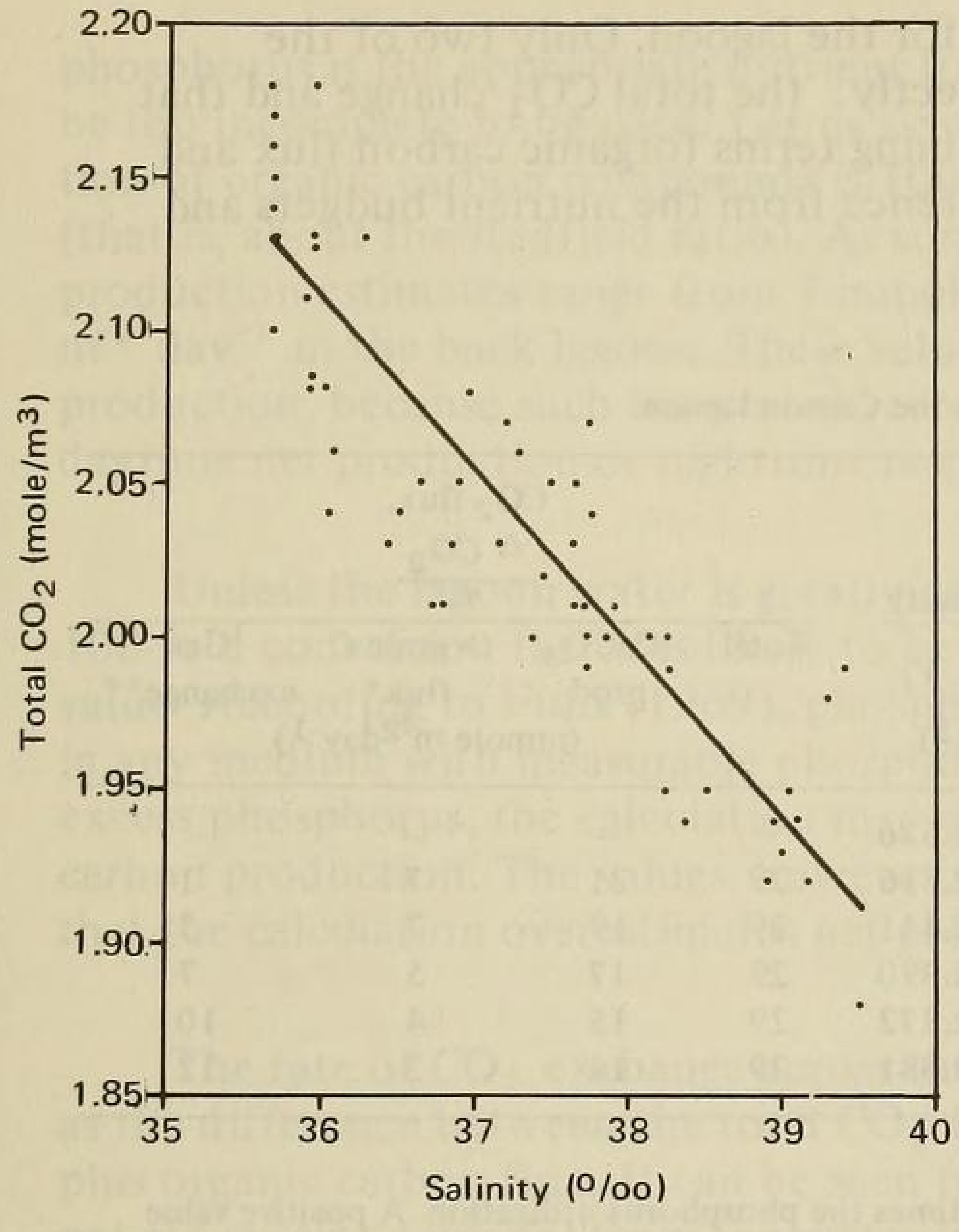

Figure 21. Total CO_2 versus salinity, including linear regression line.

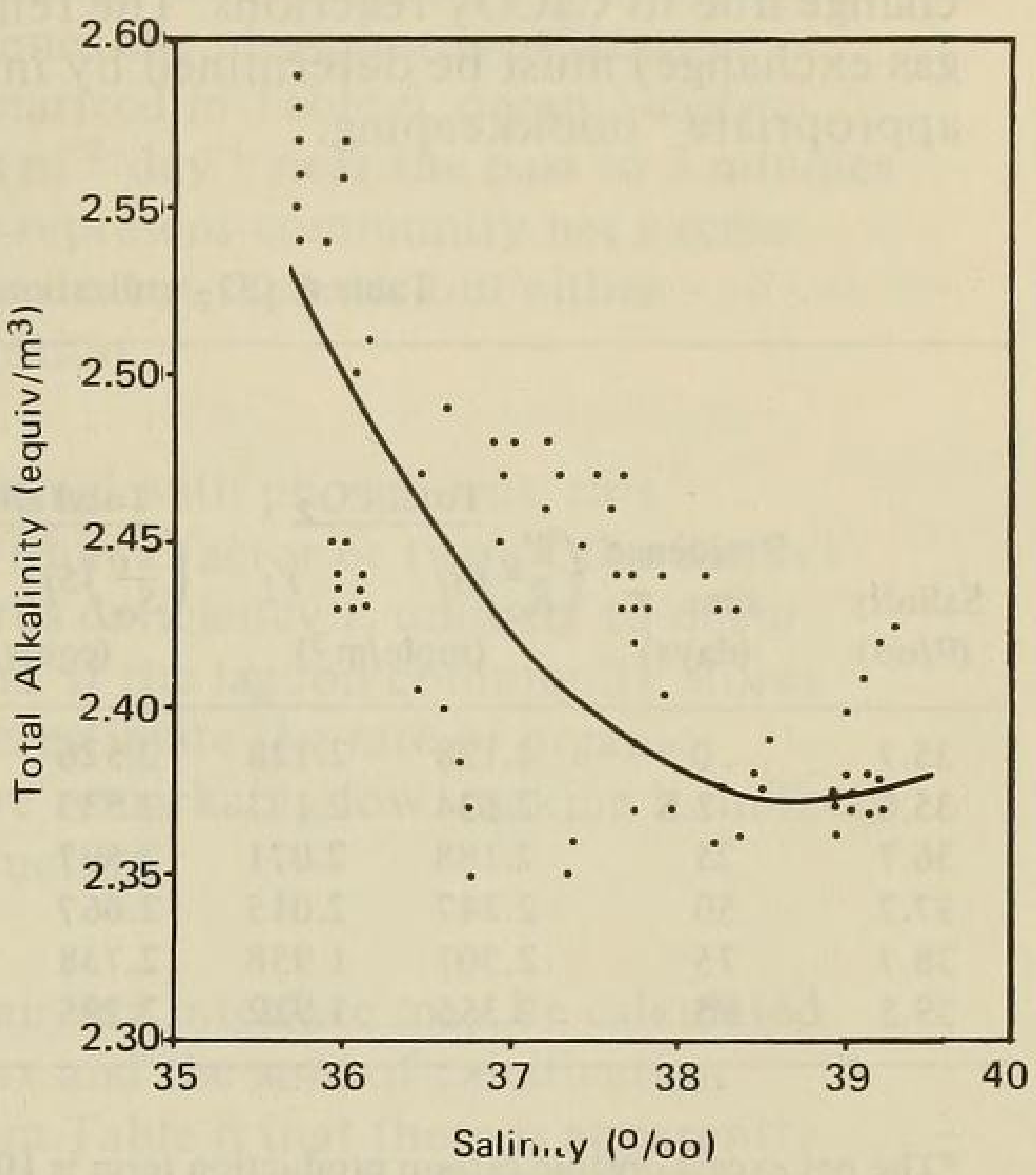

Figure 22. Total alkalinity versus salinity, including quadratic regression line.

Total alkalinity decreased from about 2.55 equiv/m^3 near the pass to about 2.4 equiv/m^3 near the back of the line reef zone. The quadratic regression equation for total alkalinity (TA) versus salinity has a coefficient of determination of 69%:

$$TA\ (\text{equiv/m}^3) \doteq 27.157 - 1.279S + 0.0165S^2 \qquad (12)$$

This descriptive equation is less satisfactory than the nutrient equations presented above, but higher-order polynomials do not improve the fit significantly. The description is least satisfactory near the lagoon pass, where the equation apparently underestimates alkalinity somewhat. The alkalinity decrease indicates that net precipitation of $CaCO_3$ was occurring in the lagoon.

One further CO_2-related parameter considered here but not mapped is CO_2 partial pressure (P_{CO_2}). The P_{CO_2} of water entering the lagoon averaged about 330 μatm, and the mean of the lagoon samples was about 290 μatm. The incoming water was very near the predicted atmospheric equilibrium value for 1973 (about 326 μatm, according to Ekdahl and Keeling, 1973). The mean value for incoming water is in substantial agreement with Keeling's (1968) world map of surface-water P_{CO_2} value in the vicinity of Canton.

Table 6 summarizes the CO_2 budget for the lagoon. Only two of the terms in the budget can be determined directly: the total CO_2 change and that change due to $CaCO_3$ reactions. The remaining terms (organic carbon flux and gas exchange) must be determined by inference from the nutrient budgets and appropriate "bookkeeping."

Table 6. CO_2 utilization in the Canton lagoon.

		Total CO_2		Total alkalinity		CO_2 flux, $\frac{\Delta CO_2}{\tau}$			
Salinity (°/oo)	Residence time, τ (days)	$\left(\frac{Y_o}{S_o}\right)S_l$ (mole/m³)	Y_l (mole/m³)	$\left(\frac{Y_o}{S_o}\right)S_l$ (equiv/m³)	Y_l (equiv/m³)	Total (mmole m⁻²day⁻¹)	$CaCO_3$ prod (mmole m⁻²day⁻¹)	Organic C flux* (mmole m⁻²day⁻¹)	Gas exchange** (mmole m⁻²day⁻¹)
35.7	0	2.128	2.128	2.526	2.526	–	–	–	–
35.8	2.5	2.134	2.123	2.533	2.516	29	21	7	1
36.7	25	2.188	2.071	2.597	2.441	29	19	7	3
37.7	50	2.247	2.015	2.667	2.390	29	17	5	7
38.7	75	2.307	1.958	2.738	2.372	29	15	4	10
39.5	95	2.355	1.912	2.795	2.381	29	14	3	12

*The net excess organic carbon production term is 100 times the phosphorus utilization. A positive value for flux indicates net production.

**A positive value for exchange indicates net evasion.

The total CO_2 change averaged 29 mmoles m^{-2} day^{-1} depletion throughout the lagoon, as can be calculated from Eq. 5 and 11. Such a constant depletion rate throughout the lagoon is obviously an oversimplified view of a more complex pattern, but the high (80%) coefficient of determination on Eq. 11 suggests that the simplification does not introduce serious errors. The molar CO_2 change due to the precipitation or solution of $CaCO_3$ equals half the equivalents of alkalinity change (Smith and Key, 1975). Hence, the CO_2 change due to $CaCO_3$ precipitation in the lagoon can be calculated using this relationship along with Eq. 5 and 12. The calculated CO_2 utilization from calcification decreased from 21 mmoles m^{-2} day^{-1} near the pass to 14 mmoles m^{-2} day^{-1} in the back lagoon. Inspection of the regression equation in Fig. 22 suggests that this calcification relationship is a satisfactory description of the high-salinity (integrated record) samples, but that the equation underestimates calcification near the pass.

Organic carbon reactions utilizing or liberating CO_2 cannot be directly calculated from the CO_2 data, but they may be inferred from the nutrient data. Redfield *et al.* (1963) give the ratio of carbon to nitrogen to phosphorus utilization or release by marine organisms to be about 106:16:1. If organic carbon flux at Canton is to be inferred from one of the nutrient budgets, phosphorus is the appropriate nutrient to consider; the nitrogen budget may be too incomplete to be used. Let us assume that CO_2 utilization in the formation of organic carbon compounds is 100 times the phosphorus utilization (that is, about the Redfield ratio). As summarized in Table 6, organic carbon production estimates range from 7 mmoles m^{-2} day^{-1} near the pass to 3 mmoles m^{-2} day^{-1} in the back lagoon. These values represent community net excess production, because such integrated records do not separate out either daytime net production or nighttime respiration.

Unless the lagoon water is greatly enriched with phosphorus, this 100-fold conversion factor is likely to be within a factor or two of the correct value. According to Fuhs (1969), phosphorus deficiency is unlikely to occur in any medium with measurable phosphorus. If the lagoon community stores excess phosphorus, the calculation may overestimate the rate of organic carbon production. The values, however, are remarkably low, making it unlikely that the calculation overestimates net production.

The rate of CO_2 exchange across the air–sea interface may be calculated as the difference between the total CO_2 flux and the sum of calcification plus organic carbon flux. It can be seen from Table 6 that there is apparently net gas evasion (escape) from the water into the atmosphere. This evasion ranges from near 0 at the pass to about 12 mmoles m^{-2} day^{-1} in the back lagoon. This net evasion provides a method for evaluating the magnitude of gross organic carbon production in the lagoon.

Up to this point, the CO_2 budget has been treated in terms of day-to-day net changes, without direct regard for diurnal CO_2 variations from daytime net production and nighttime net respiration. Yet there is undoubtedly a diurnal variation in total CO_2 and P_{CO_2}, in response to the diurnal metabolic cycles (Schmalz and Swanson, 1969; Smith 1973; Smith and Pesret, 1974). Although the daytime P_{CO_2} averages 290 μatm, the gas exchange term of the budget indicates that the 24-hour mean P_{CO_2} must be something above 326 μatm in order to effect net evasion. Smith and Pesret (1974) summarized available data and suggested that the most appropriate CO_2 gas exchange rate coefficient for seawater is about 0.6 mmole m^{-2} day^{-1} for each μatm difference between the air and water. To account for mean evasion rate of 12 mmoles m^{-2} day^{-1}, the above coefficient demands that the 24-hour mean P_{CO_2} be approximately 20 μatm above the equilibrium value, or about 345 μatm. A nighttime mean P_{CO_2} of about 400 μatm, averaged with the daytime mean of 290 μatm yields the appropriate 24-hour average. It can be calculated that this day-to-night P_{CO_2} difference is equivalent to about 0.08 mmole/m^3 total CO_2 difference, or about 0.5 mole/m^2 through a 6.2-m water column. This relatively small diurnal range is comparable to the range observed by Smith and Pesret (1974) during a 24-hour sampling period in the lagoon at Fanning.

This mean day-to-night difference is the difference between daytime net organic carbon production and nighttime respiration. If daytime respiration equals nighttime respiration (the assumption which is almost universally made), then the CO_2 difference between day and night equals gross organic carbon production: 0.5 mole m^{-2} day^{-1}, or 6 gC m^{-2} day^{-1}. Moreover, the near-zero net excess production rate (Table 6) indicates that the 24-hour respiration rate is approximately the same as the gross production rate. That is, the gross production-to-respiration ratio of the lagoon community is near 1.0.

An alternative interpretation of the apparent CO_2 evasion against a P_{CO_2} gradient is that an error in the organic carbon term of the CO_2 budget may have carried over into the gas exchange term. That explanation is unlikely. If no gas evasion occurs, then net excess organic carbon production must be low by a factor of 5 (Table 6). In turn, that error would imply a C:P ratio of over 500:1 for the organic material being produced in the lagoon. Such a ratio would indicate extreme phosphorus limitation to production—far beyond the highest C:P ratios obtained for algal cultures in phosphorus-deficient media (Fuhs, 1969; Ketchum and Redfield, 1949). Yet Fuhs has said that any culture medium with measurable phosphorus is unlikely to be limited by that nutrient. Moreover, the observed N:P ratio (about 8.5; Table 5) does not suggest any such phosphorus limitation.

Budget of Particulate Material Flux

It is also possible to estimate the magnitude of suspended-load transfer between the open ocean and the lagoon. Water in the Canton lagoon is very turbid. This turbidity was documented by Secchi disc readings and by measurements of percent light transmission through a 1-m water column (Fig. 23). It can be seen that the Secchi disc reading decreased by about 1.5 m for each 10% reduction in light transmission. The combined data from 1972 and 1973 yielded a mean Secchi disc reading (Fig. 24) of about 5 m, corresponding to 33% light transmission through a 1-m water column. The maximum turbidity in the lagoon corresponded to 10% light transmission, and the clearest water (near the pass) had 58% light transmission.

In order to determine the major contributors to the turbidity, the suspended $CaCO_3$ content and chlorophyll *a* content of 13 water samples were compared with the light transmission data. Figure 25 shows an apparent negative exponential relationship between $CaCO_3$ and light transmission but no relationship between chlorophyll and transmission. Thus, suspended $CaCO_3$ appears to be the major contributor to the lagoon turbidity. The mean $CaCO_3$ content of the water was about 500 mg/m^3, while the mean chlorophyll *a* content of the water (including a number of samples not illustrated here) was 0.8 mg/m^3. It is assumed to a first approximation that both of these parameters are near 0 in the ocean water.

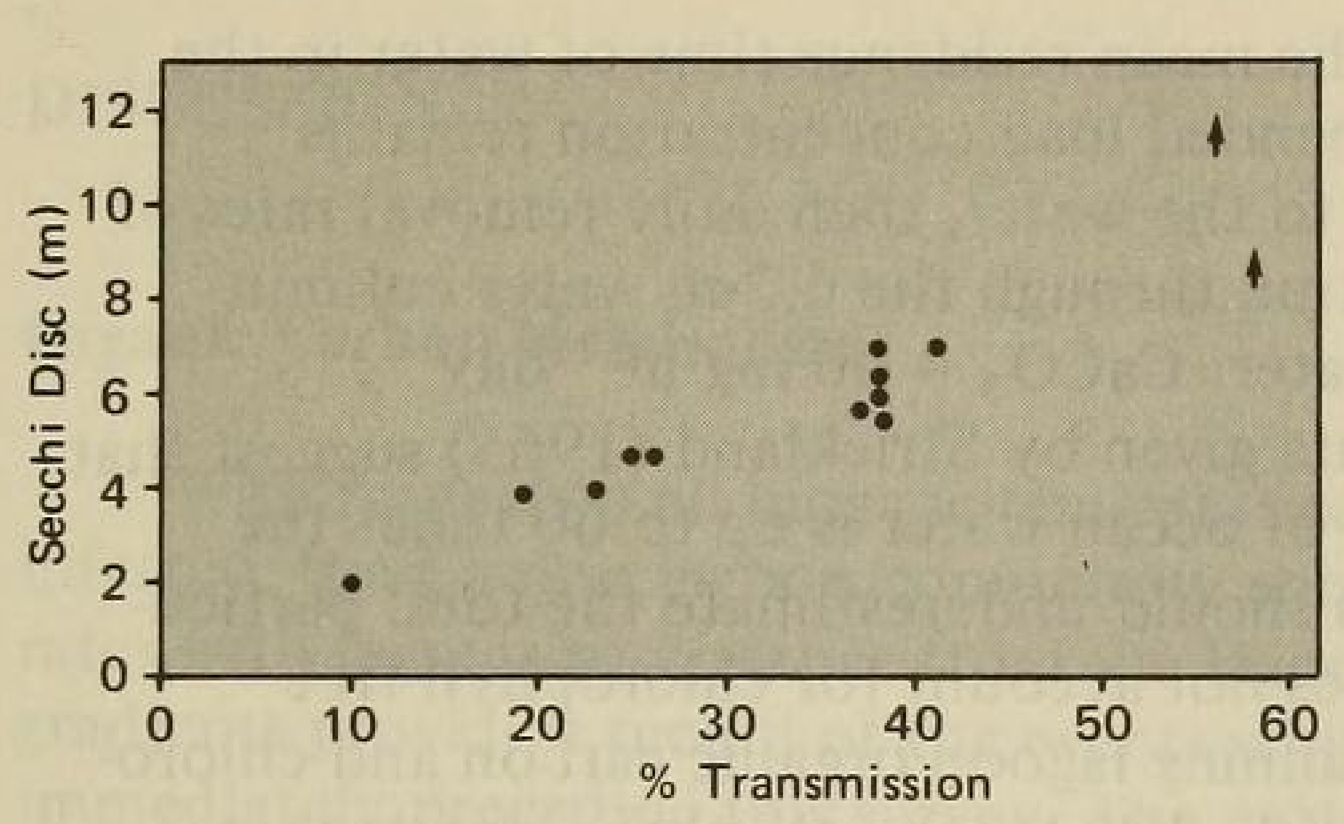

Figure 23. Secchi disc reading versus percent light transmission through a 1-m water column. (For samples indicated by arrows, the Secchi disc was visible on the sea floor.)

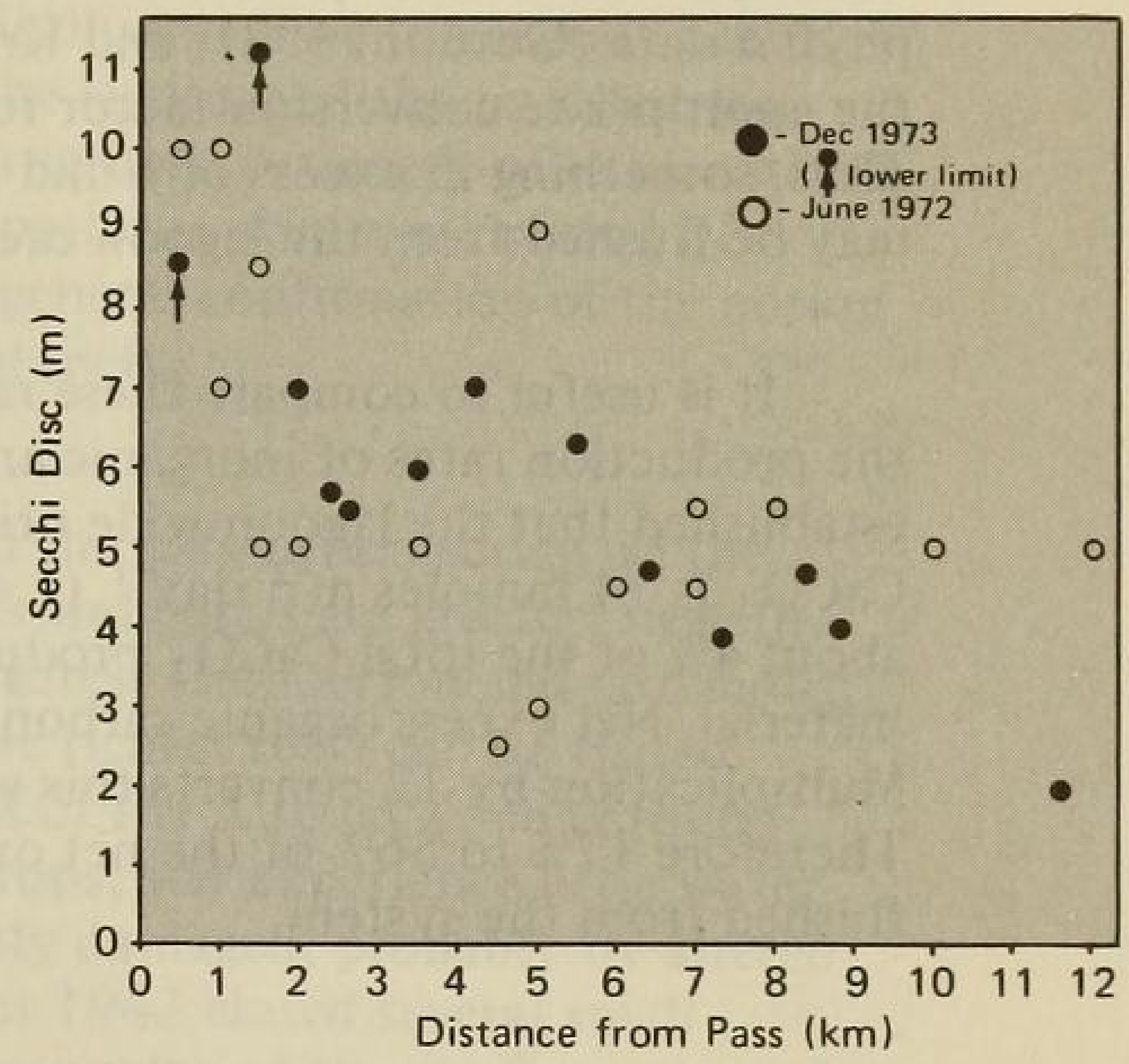

Figure 24. Secchi disc reading versus distance from the lagoon pass.

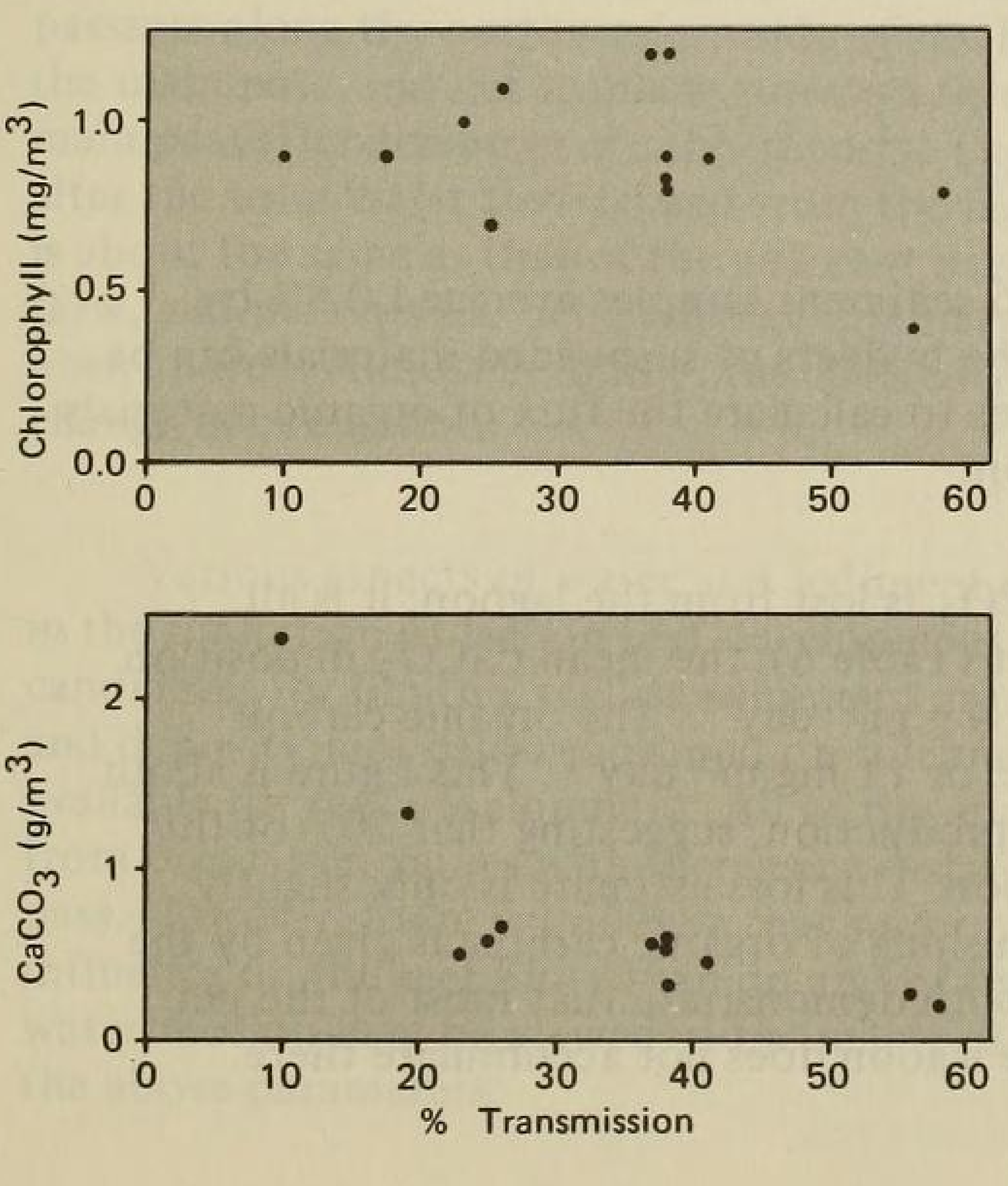

Figure 25. Chlorophyll *a* and suspended $CaCO_3$ versus percent light transmission through a 1-m water column.

Previous calculations have given the mean residence time of water in the lagoon to be about 50 days. If the suspended load concentration remains constant and is flushed proportionally to the water, then daily removal rates of these materials will be their concentration through the 6.2-m water column divided by the residence time of the water: $CaCO_3$ = 60 mg m^{-2} day^{-1}; chlorophyll *a* = 0.1 mg m^{-2} day^{-1}. Data given by Strickland (1965) suggest that the particulate organic carbon content of ocean water is up to 60 times the chlorophyll *a* content. This conversion should underestimate the total particulate organic carbon load, because it does not account for chlorophyll-free detrital material. Comparison of the Fanning lagoon organic carbon and chlorophyll *a* data (Gordon, 1971, and Krasnick, 1973, respectively) suggests that the appropriate conversion factor for lagoon systems may be as high as 200. Thus, something in excess of 6 and perhaps as much as 20 mg organic C/m^2 may be flushed from the lagoon each day.

It is useful to compare these rates of particulate-matter flushing with the production rates of inorganic and organic carbon. The budget in Table 6 established that the lagoon-wide utilization of CO_2 for net precipitation of $CaCO_3$ is 14 mmoles m^{-2} day^{-1} (1.4g $CaCO_3$ m^{-2} day^{-1}). It appears that only about 4% of the total $CaCO_3$ produced in the lagoon escapes as suspended material. Net excess organic carbon production is about 3 mmoles m^{-2} day^{-1}. Multiplication by 12 converts this value to mg organic carbon: 36 mg m^{-2} day^{-1}. Therefore 17% to 56% of the net organic carbon production appears to be flushed from the system.

Organic Material in Lagoon Sediments

The organic carbon content of 16 sediment samples averaged 0.8% by weight (standard deviation = 0.4%). The budgets of suspended materials can be used with these organic carbon analyses to calculate the flux of organic materials into the sediments and from the lagoon.

To a first approximation, no $CaCO_3$ is lost from the lagoon; it is all deposited there. From the CO_2 budget (Table 6), the mean $CaCO_3$ deposition rate in the lagoon is therefore about 1.4 g m^{-2} day^{-1}. The organic carbon deposition is about 0.8% of this figure, or 11 mg m^{-2} day^{-1}. This figure is about 30% of the net excess organic carbon production, suggesting that 70% of this production must be lost from the lagoon. This loss estimate is only slightly higher than the upper figure for the flushing of organic carbon as given by the suspended-load data. The two values both demonstrate that most of the net excess organic carbon produced in the lagoon does not accumulate there.

DISCUSSION

Organic Carbon Metabolism

With respect to all biogeochemical flux parameters either measured or inferred, the Canton lagoon community shows distinct gradients of decreasing rates with increasing distance from the lagoon pass. These biogeochemical gradients provide a record of the events which occurred in the lagoon during and immediately preceding this survey. The patterns observed are in general accord with both the present distribution of biota in the lagoon and the past distribution as inferred from the distribution of reef structures. A variety of explanations might be offered for the maintenance of these patterns over some period of time. We suspect, however, that the pattern is general confirmation of the notion that water movement favors the growth of coral reefs.

There are clues that water motion is, of all the parameters acting on the system, the major one. Standing crops of fishes and corals are greatest near the pass, where tidally induced water flow is the greatest (Henderson and Grovhoug, this report; Jokiel and Maragos, this report). The richest reefs can be visited safely only during slack tides. By contrast, reefs of the Altered Zone (Frontispiece) are low in both fish and coral standing crops, and experience little water motion. These reefs have obviously been recently damaged, probably by altered circulation. Extensive dredging operations about 1943 closed several small passages along the northwestern side of the lagoon, altered the configuration of the main pass, and cut seaplane runways through patch and line reefs near the main pass (Henderson *et al.*, this report). These operations apparently did not alter the total water flow to and from the lagoon; the present lagoon tidal range is about the same as that of the adjacent ocean. However, the patterns of water flow, and perhaps the net exchange rate between the ocean and the lagoon, have been altered. Almost certainly, the Altered Zone has experienced the greatest change in circulation.

Various aspects of water and sediment composition might be implicated in the limitation of lagoon reef development at Canton. The most conspicuous candidates for limiting reef development are salinity, nutrients, turbidity, light, and deposition of calcareous mud on substrata which might otherwise be available for reef development. All of the above properties progressively deviate from ocean-reef values with increasing distance into the lagoon from the single pass. However, there is evidence that water motion exerts a more direct influence on the reef biota than do any of the above variables. Indeed, decreasing water motion may be viewed as the major cause for the gradients observed in the above parameters.

The lagoon salinity ranges from about 36 to 40 o/oo, outside the 34–36 o/oo range considered by Wells (1957) to be optimal for coral growth. Yet, luxuriant reefs in the Red Sea at salinities up to 42 o/oo have been reported by Loya and Slobodkin (1971).

Both nitrogen and phosphorus are often considered to be materials which may limit metabolic activity of biological systems. The data presented here suggest that the net uptake ratio of dissolved inorganic nitrogen and phosphorus from the lagoon water (8.5:1) is slightly above the relative ratios of those materials in the water entering the lagoon (about 6.4:1); that is, if this uptake rate were maintained, nitrogen would be exhausted slightly before phosphorus. We suspect that neither of these materials alone limits metabolism in the Canton lagoon, nor perhaps in most other coral reef ecosystems.

Turbidity, light, and the deposition of fine sediments represent a complex interaction of factors which have been suggested to limit reef development in other areas. Analogy with the reefs in the lagoon of Fanning Atoll suggests that such limitation is not the case at Canton. Roy and Smith (1971) report that the Fanning lagoon reefs are much richer than those at Canton; yet the water is actually more turbid at Fanning. Calcium carbonate production rates in the two systems (Smith and Pesret, 1974; this paper) suggest that the sediment production rate, and by implication the deposition rate, is perhaps twice as fast at Fanning as at Canton.

Water motion has been suggested by Munk and Sargent (1954), Wells (1954), and many other authors to be an important variable in the development of coral reefs. Riedl (1971) argues that water motion is not an environmental parameter in its own right but is a transportation medium for other materials. A variety of suggestions has been offered to explain the roles of water motion in favoring the growth of coral reefs. Perhaps the most recurrent of these suggested roles have been that the flow of water supplies food, aids in the diffusion of dissolved materials, dissipates heat, transports larvae, removes waste products, and alleviates smothering by sediments. All of these suggestions are undoubtedly valid, and the list could be expanded.

Water motion also provides a substantial subsidy of energy to an ecosystem in addition to that provided by solar radiation. The tidal energy to change the water level in the Canton lagoon may be calculated to be about ten times the caloric input from net organic carbon production,* and energy input into the

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*The input of tidal energy may be approximated by the formula for kinetic energy (K): K equals the mass of water raised or lowered times the acceleration of gravity times the height the water is raised or lowered. The mass of the tidal head per square meter is 700 kg, and the water is raised and lowered twice the mean tidal range (0.7 m) daily. So K is 19×10^4 joules m^{-2} day^{-1}, or about 5 Kcal m^{-2} day^{-1}. The energy associated with a net organic carbon production of 40 mg C m^{-2} day^{-1} is about 10 Kcal per gram of carbon, or 0.4 Kcal m^{-2} day^{-1} (Whittaker and Likens, 1973).

lagoon by wind stirring is not even numerically considered here. Even if only a small percentage of this mechanical energy can be utilized by organisms which would otherwise either move water or move through it in order to serve the roles enumerated above, this subsidy is substantial. In the absence of adequate evidence to demonstrate which aspects of water motion might be the most important, its function may be viewed as that of a generalized transfer coefficient. In any water mass, increased motion will enhance the transfer of materials used or discarded by the biota. This transfer may be considered a subsidy to input of solar radiation. The input of mechanical energy is not evenly distributed throughout the lagoon. Clearly, tidal energy decreases with distance from the pass, and wind energy decreases with water depth. Thus, shallow reefs near the pass are favored by this energy subsidy. Local depressions in the shallow reefs most effectively "channel" the flow of water and support vigorous reef communities. In some portions of the seaward reefs, water motion (energy) may be so great that organisms are excluded or destroyed by mechanical damage. For example, Munk and Sargent (1954) report a mean annual discharge of 8 hp/ft of reef front against the northeast (windward) face of Bikini Atoll. If this power is dissipated over a depth of 20 m on a 30-degree slope (that is, to approximately the 10-fathom terrace), then it is equivalent to an energy input of about 10^4 Kcal m^{-2} day^{-1} against that face—about 2,000 times the mean energy input we postulate for the Canton lagoon. Examination of a windward fore-reef spur at Enewetak Atoll demonstrates these spur and groove structures to be largely the product of erosion (Buddemeier *et al.*, 1975), at least to water depths of about 5 m.

The budget of organic carbon production does not indicate what component of the community is principally responsible for the production. It seems likely that even in the lagoon primary production is dominated by the benthos. In summarizing plankton production rates for reef lagoons, Gordon *et al.* (1971) reported no value higher than about 1 g C m^{-2} day^{-1}. If a gross production-to-respiration ratio of 2 is assumed for plankton communities, then this net production is equivalent to a gross production of about 2 g C m^{-2} day^{-1}. This figure is substantially below the gross production rate calculated for Canton (6 g C m^{-2} day^{-1}). It therefore seems likely that the plankton are not the major producers of that lagoon community.

Canton and indeed several other atolls throughout the equatorial Pacific Ocean are exposed to some of the highest major inorganic nutrient levels to be found in open ocean surface waters (compare the phosphate map of Reid, 1961, with the coral-reef distribution map of Wells, 1957). Under such circumstances it is reasonable to suppose that neither phosphorus nor nitrogen would limit reef metabolism. Alternative micronutrients are demonstrably important to the productivity of phytoplankton in the open ocean (for example, iron; Menzel and Ryther, 1961), and have been suggested to be important in the distribution of some reef algae (for example, *Sargassum*; Doty, 1954; DeWreede, 1973).

These micronutrients might not correlate well with nitrogen and phosphorus, because the micronutrients are largely supplied from local sources, such as the trace metals found in the rocks of high volcanic islands.

Available data suggest that the productivity of atolls is probably similar to that of high-island reefs (compare the data in Marsh, 1974, and Kohn and Helfrich, 1957, with the summary data in Smith and Marsh, 1973). Critical materials may be cycling more rapidly within atoll systems than high-island reefs. Grazing activity (for example, by fishes; Bakus, 1969) is of considerable importance in this recycling—perhaps far beyond the energetic importance of the organisms in question.

The dissolved inorganic nitrogen and phosphorus budgets of the Canton lagoon both show that the community utilizes these materials, hence that the community is autotrophic. The slowness of the net uptake rates in comparison to the high gross production rate demonstrates that the margin of community autotrophy is remarkably slender. In fact, the low net excess production observed for the total lagoon (about 40 mg C m^{-2} day^{-1}) is somewhat below the frequently quoted net production rate for the open ocean (100 mg m^{-2} day^{-1}; Ryther, 1969). Because of the high oceanic nutrient levels near Canton, the net excess production of the ocean planktonic community there may well exceed this value by a considerable margin.

Despite the very low net excess production of the Canton lagoon community, there apparently is net export of organic carbon from the atoll to the open ocean. This conclusion is supported both by the composition of materials suspended in the water column and by the sediment composition. If there were not such export, the sediments should have about 2.5% by weight organic carbon; instead, they average about 0.8%. In constructing a carbon budget for the Bahama Banks, Broecker and Takahashi (1966) noted an apparent discrepancy between the budgetary implications of net organic carbon production and the observed sediment composition. They concluded that their budget was not properly balanced. This does not seem to be the case at Canton, and it may not have been true for the Bahamas budget either. The suspended-load data discussed here suggest that there may be substantial removal of organic material from the lagoon, with relatively little $CaCO_3$ loss. A variety of explanations might be offered for this phenomenon; those given below seem the most reasonable.

In the first place, $CaCO_3$ precipitated by the benthos in the lagoon is less likely than organic carbon to be dislodged from the lagoon floor by either mechanical or biological activity and then to become suspended in the water column. Organic material, once suspended, is less dense than the $CaCO_3$ and will stay in suspension longer. Hence, particulate organic carbon is more susceptible to flushing from the system than is inorganic carbon. Moreover, one major component of the organic carbon inventory in the lagoon has not even been evaluated in these budgets—dissolved organic carbon. This material would also be easily flushed from the system. Indeed, it would be surprising if there were not more organic carbon lost than inorganic carbon.

The suggested export of up to 70% of the excess organic carbon produced in the lagoon makes the narrow autotrophic margin of the lagoon community all the more remarkable. Most of the excess production which does occur does not accumulate but leaks from the system. The gross organic carbon production of the Canton lagoon is almost 10^5 tons/yr. The net excess organic carbon production of the lagoon amounts to approximately 550 metric tons/yr. Of that net production, about 400 tons is lost to the ocean, and the remainder (0.2% of the gross production) accumulates with sediments on the lagoon floor.

Depositional History

The $CaCO_3$ production rate in the lagoon is about 500 g m^{-2} yr^{-1} (Table 6). This rate is about 10 to 15% of the rates which have been reported by the same alkalinity-depletion technique for reef flats (Smith, 1973; Kinsey, 1972), about half the rate found in the Fanning Atoll lagoon (Smith and Pesret, 1974), and the same as the rate reported by Broecker and Takahashi (1966) for the Bahama Banks. If it is assumed that the sedimentary materials being produced have a dry-weight density of about 1.4 g/cm^3 (that is, about 50% porosity), and that none of the material being produced is lost from the lagoon, then this production rate at Canton is equivalent to a mean vertical deposition rate of about 0.3 mm/yr. World-wide mean sea level is presently changing little, if at all (Curray *et al.*, 1970); there is no reason to suspect that large vertical tectonic movements have occurred at Canton.* Therefore, the lagoon floor at Canton is probably not shoaling by more than this small increment. There probably is a balance between "too much" production on the reefs and "too little" production on the lagoon floor. Erosion (largely biological) allows redistribution of materials throughout the lagoon.

Prior to about 8,000 years ago, sea level was rising at a rate approaching 2 cm/yr (Curray *et al.*, 1970). Under such conditions, it is inconceivable that reefs resembling those presently found in the Canton lagoon could have produced sufficient sediment to maintain the lagoon floor at a constant depth

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*There are morphological features which suggest that there may have been as much as a 2-meter high-stand (possibly local) of sea level at Canton within the last several thousand years. This uncertainty is within the range of present debate about eustatic changes and is of no direct concern here.

relative to the rising sea level. In fact, even if such reefs were not being eroded, they probably still could not have maintained themselves at sea level. Yet the reef structures probably do not greatly antedate the present general island morphology. The shape of the reefs appears related to water flow to and from the lagoon.

The entire reef configuration in the lagoon today therefore appears to be less than 8,000 years old, and these reefs have probably grown up from a base approximated by the present maximum depth found in the lagoon (about 25 m). Topographic details of the base cannot be inferred from the present topography. This amounts to a lagoon infilling of about 20 m in 8,000 years, or an average of 2.5 mm/yr.

If this interpretation is substantially correct, then the growth of the reefs in the lagoon has slowed considerably as the lagoon has become clogged with reef structures. One or more passages have existed along the southeast rim of the atoll until relatively recently and have been blocked by the formation of beach ridges or by slight oscillations in relative sea level or by both. The maximum initial rate of reef growth making this model feasible is about 5 mm/yr if the slowdown from that maximum rate has been constant with time. This maximum rate is consistent with the rates which Smith (1973) and Kinsey (1972) have reported for shallow reef environments elsewhere.

Mechanisms governing $CaCO_3$ production rate in the Canton lagoon are probably similar to those which limit organic carbon production. Corals are the most conspicuous calcifying organisms in the lagoon, if not the major ones. The distribution of corals obviously is sensitive to location (Jokiel and Maragos, this report). The growth rates of a few individual coral heads from Canton have been determined by means of x-radiography (R. Buddemeier, personal communication), and these rates do not appear to be directly sensitive to the location from which the coral was collected. Hence, the $CaCO_3$ production rate of the lagoon seems more nearly related to the standing crop of calcifying organisms than to variations in the calcification rates of individual taxa.

The Canton lagoon CO_2 system bears one major contrast with that of Fanning lagoon. Fanning lagoon water was found to be approximately saturated with aragonite, and that saturation state was suggested as a possible factor limiting the $CaCO_3$ production rate there (Smith and Pesret, 1974). At Canton, the calculated saturation state of the water with aragonite remains relatively constant throughout the lagoon, near 200% saturated ($CaCO_3$ ion activity product $\approx 10^{-7.9}$). It thus appears that the rate at which $CaCO_3$ is precipitated in that lagoon approximately matches the increase in $CaCO_3$ ion activity product from evaporation.

SUMMARY AND CONCLUSIONS

Much of the budgetary analysis presented here is highly speculative, and this speculation is offered without apology. The budgets provide a rapid overview of a poorly known environment which constitutes a major portion of coral atolls. Such an overview gives little attention to biological detail; that detail can follow, using the overview as a framework on which to build.

This investigation was undertaken as part of an environmental survey of the Canton lagoon. The budgets provide bases for environmental assessment. The major environmental characteristics suggested by the budget are summarized below.

Evaporation, rainfall, and salinity provide the basis for estimating the residence time of water in the lagoon. Salinity increases from net evaporation as water ages in the lagoon. The mean residence time of water in the lagoon is about 50 days, while the oldest water remains in the lagoon about 95 days.

The productivity of the Canton lagoon community is probably not limited by the major inorganic plant nutrients (nitrogen and phosphorus). Both of these materials are present at high concentrations in water entering the lagoon, and neither is exhausted while the water ages in the lagoon. The net utilization of nutrients demonstrates that the lagoon community is autotrophic, and the slow rate of utilization demonstrates that the margin of autotrophy is narrow. Lagoon-wide phosphorus utilization is about 0.027 mmole m^{-2} day^{-1}, and nitrogen utilization is about 8.5 times this rate.

Net organic carbon production can be inferred from the phosphorus budget to be about 3 mmoles m^{-2} day^{-1}, or about 36 mg C m^{-2} day^{-1}. This rate is probably near the net organic carbon production of the open ocean adjacent to the atoll. Gross organic carbon production is about 6 gC m^{-2} day^{-1}, comparable to rates which have been estimated for coral reef flats elsewhere and over 100 times the net production. Thus, the lagoon maintains a remarkably close balance between the production and consumption of organic compounds. Both the suspended load and the sediments suggest that most of this small excess of organic carbon which is produced is flushed from the lagoon rather than being incorporated into the sediments. Yet the amount of flushed material is a trivial fraction of the gross production.

The rate at which the lagoon community produces calcareous material is much slower than $CaCO_3$ production rates reported for other portions of coral atolls. It appears likely that the lagoon reefs have developed within the last 8,000 years and have filled the lagoon with up to 20 m of sedimentary materials.

The standing crop of organisms in the lagoon is obviously related to local variations in water motion within the lagoon. Net and gross organic carbon production and the production of $CaCO_3$ are also apparently related to this motion. Aside from purely mechanical destruction, the only extensive human damage to the lagoon community appears to be associated with local reduction of water motion within the lagoon. Such artificial damage is minor in comparison with the pervasive geological history of progressive lagoon infilling, enclosure, and restriction of circulation.

Perhaps the most conspicuous attribute of the Canton lagoon material balance is the efficiency with which the system retains materials once formed. In the case of organic materials, this retention is accomplished by virtually complete recycling of materials, with almost no loss of these materials back to the open ocean or to the sediments on the lagoon floor. The small loss which does occur is balanced by the continued uptake of materials from ocean water which flows into the lagoon. Inorganic materials are precipitated and deposited, leading to a gradual infilling of the lagoon with calcareous sediments.

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