

THE DISTRIBUTION OF NUTRIENTS IN THE COSTA RICA DOME IN THE EASTERN TROPICAL PACIFIC OCEAN

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ABSTRACT

The distributions of salinity, dissolved oxygen, phosphate, nitrate, and silicate in the Costa Rica Dome are described from data collected during the Costa Rica Dome cruise November–December 1959. The dome is an area where nutrient-rich, oxygen-poor water is brought to the surface by upwelling.

The ratios of change of oxygen, phosphate, and nitrate are computed statistically from the observed data to 1,100 m depth.

A simple mixing model is used to explain the observed vertical distribution of oxygen above 65 m when allowances are made for photosynthetic oxygen production. The contributions of oxygen from various sources are estimated by use of the model. A similar model is used to compute the ratios in which nutrients are assimilated by phytoplankton.

INTRODUCTION

The Costa Rica Dome (Cromwell 1958) is an area approximately 400 km in diameter centered near 8° N lat, 89° W long, in the eastern tropical Pacific Ocean where the isothermal surface layer is extremely shallow. Wyrcki (1964) has described the physical oceanography of this area on the basis of observations made during the Costa Rica Dome cruise, November–December 1959 (Scripps Institution of Oceanography 1960) (Fig. 1), and he has suggested a mechanism that maintains upwelling in the dome. His results are summarized below.

The anticyclonic thermal structure, or dome, is located at the eastern extremity of the thermal ridge that separates the North Equatorial Countercurrent from the North Equatorial Current. Wyrcki states that the dome may be caused by the northward deflection of the countercurrent as it impinges on the coast of Central America, causing a redistribution of mass that is effected by divergence and crosscurrent flow. He has computed an average ascending velocity within the dome of 10^{-6} m/sec and has estimated that the upwelling originates between depths of 75 and 200 m. The northward transport across the eastern limb of the dome was about 20×10^6 m³/sec, whereas the vertical transport or upwelling was only 7×10^4 m³/sec. The dome has been observed several times and appears to

be a permanent feature, although it may vary seasonally in magnitude and position.

The upwelling had a pronounced effect on the distribution of properties at the sea surface (Figs. 2b, c, d). Surface manifestations of the ascending motion were the higher salinities, lower oxygen contents, and higher nutrient concentrations in the surface water in the dome than in the surrounding surface waters.

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METHODS

During the Costa Rica Dome cruise, 6 November through 14 December 1959, 50 hydrographic stations were occupied in the area of the dome (Fig. 1). At all stations, salinity, temperature, dissolved oxygen, and inorganic phosphate were observed to at least 1,000 m. At 16 of these stations, inorganic nitrate, nitrite, and reactive silicate were observed. In addition, 8 shallow stations were occupied, and 48 surface samples were taken in the vicinity of Cocos

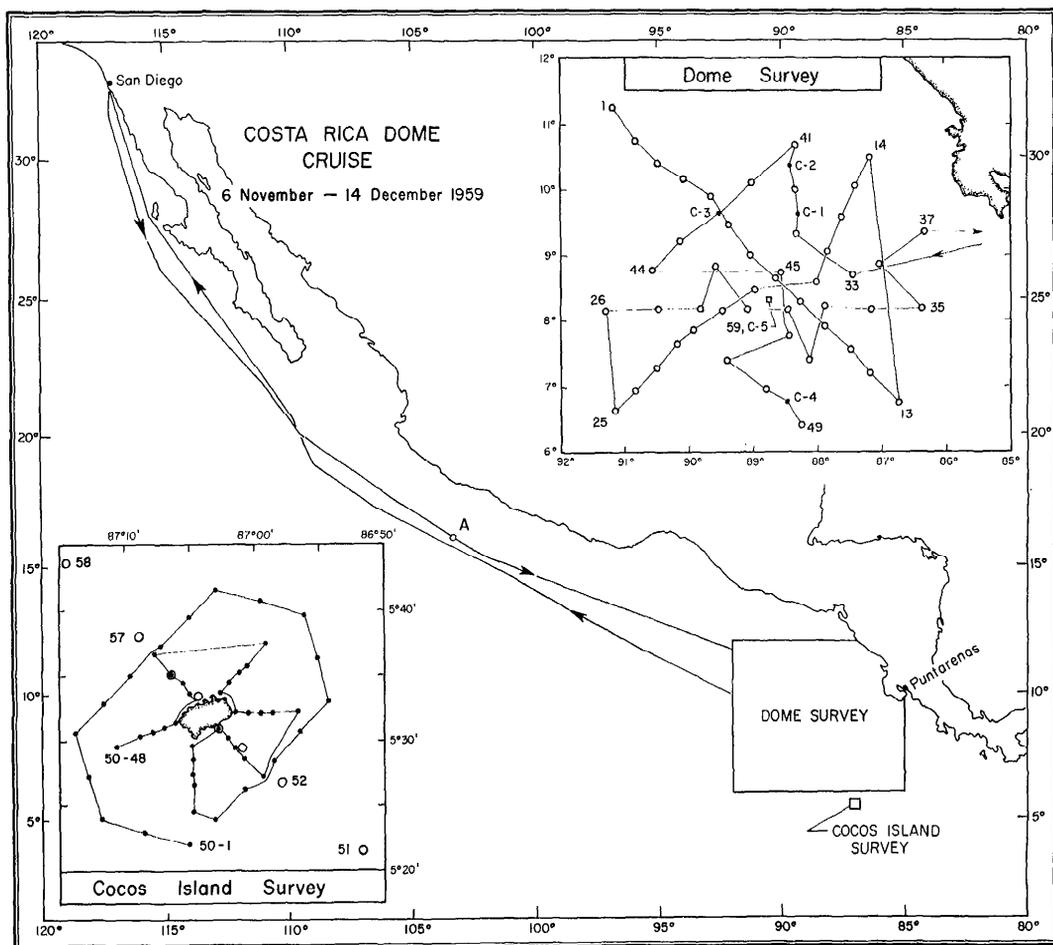


FIG. 1. Track chart of Costa Rica Dome cruise, 9 November to 14 December 1959.

Island, about 275 km south of the dome's center.

Dissolved oxygen analyses were done by the Winkler method, and oxygen solubilities were based on the solubility data of Truesdale, Downing, and Lowden (1955). Inorganic phosphate concentrations were determined by the method described by Strickland and Parsons (1960), and temperature corrections were applied as described by Wooster and Rakestraw (1951). Samples for nitrate, nitrite, and silicate were frozen aboard ship and later analyzed ashore using methods described by Strickland and Parsons (1960). Productivity measurements were made using the C^{14} technique of Steemann Nielsen (1952).

VERTICAL DISTRIBUTIONS

A characteristic of the eastern tropical Pacific is the shallow, mixed surface layer. It is only 20–30 m deep near the American coast and increases in depth to 50–70 m at 130° W long (Wyrski, in press). This shallow thermocline is probably a consequence of a general ascending motion throughout the eastern tropical Pacific north of the equator that is caused by surface waters being driven westward by persistent northeast trade winds. Extremely high nutrient and low oxygen concentrations are found in the intermediate water in this area, demonstrating that this water has undergone chemical change due either to a long residence or to an abundance of oxidizable ma-

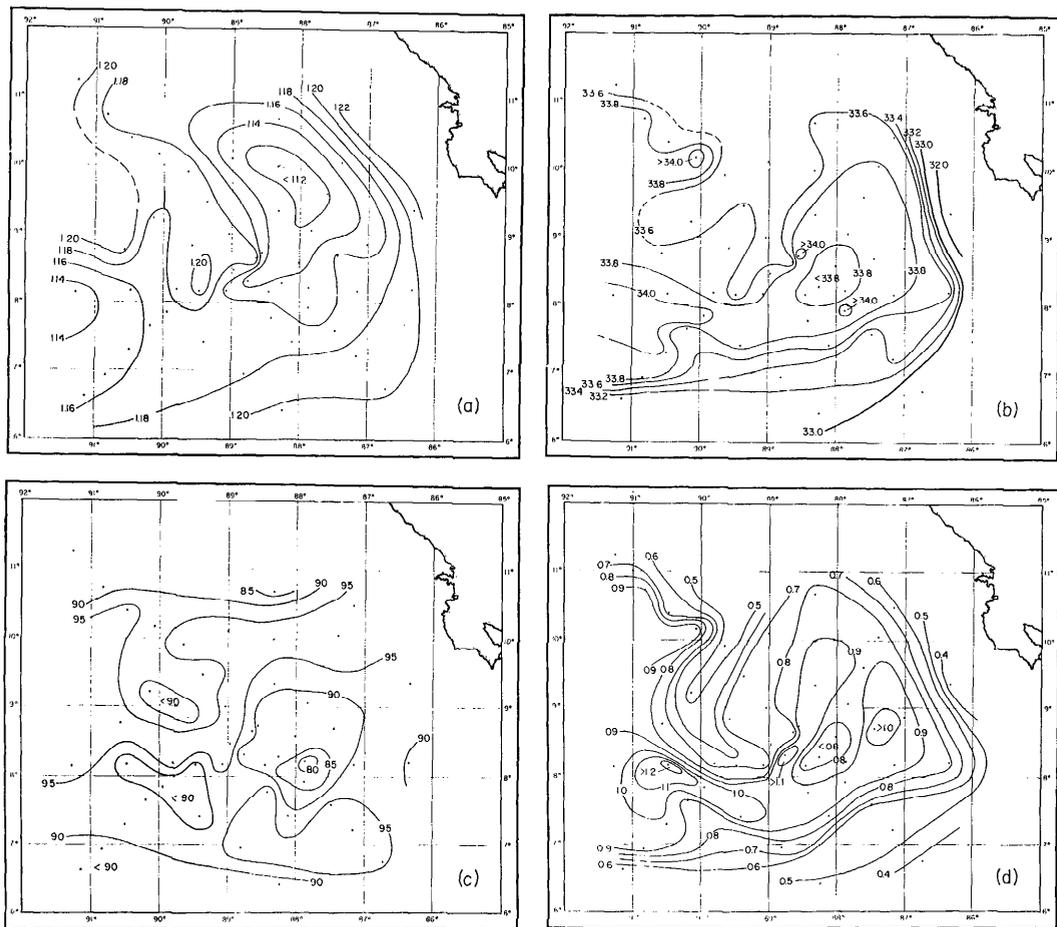


FIG. 2. Distribution of properties at the surface during Costa Rica Dome cruise, November–December 1959: (a) Geopotential topography of the surface relative to 1,500 decibars, dynamic m; (b) Surface salinity, ‰; (c) Surface oxygen, % saturation; (d) Surface phosphate, $\mu\text{g-at./liter}$.

terial in the overlying water. The distributions of chemical properties in the Costa Rica Dome are of particular interest because nutrient-rich water is readily accessible to primary producers in the dome, where the mixed layer was absent or, at most, only 10 m deep at the time of this survey.

In the dome, the inorganic phosphate concentration increased from $0.75 \mu\text{g-at./liter}$ at the surface to $2.13 \mu\text{g-at./liter}$ at 50 m. A correspondingly sharp oxygen gradient was also observed, the oxygen decreasing from 4.25 ml/liter at the surface to 1.04 ml/liter at 50 m (Fig. 3). During the cruise, the sea surface was undersaturated

with oxygen at every station (Fig. 2c), although the surface waters in the eastern tropical Pacific Ocean are generally supersaturated (Bennett 1963). The widespread occurrence of low oxygen concentrations at the surface demonstrates the intensity of upwelling in the dome.

The oxygen minimum, containing undetectable amounts of oxygen in some cases, was found at about 500 m, and the phosphate maximum, $3.4\text{--}3.5 \mu\text{g-at./liter}$, was found at 1,000 m. The maximum apparent oxygen utilization (AOU), the difference between the equilibrium oxygen solubility at 1 atm pressure, the *in situ* temperature and salinity, and the observed oxygen con-

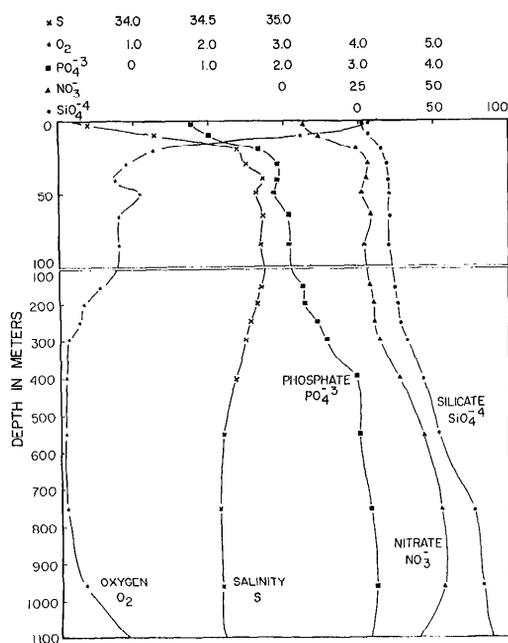


FIG. 3. Vertical distribution of oxygen, phosphate, nitrate, silicate, and salinity in the Costa Rica Dome (Station 18, 8°35' N lat, 88°00' W long). Oxygen in ml/liter, nutrients in $\mu\text{g-at./liter}$, salinity in ‰.

centration (Redfield 1942), was at about 800 m.

The vertical distribution of nitrate shows the same general features as the phosphate distribution. The nitrate concentration was about 6 $\mu\text{g-at./liter}$ at the surface and 29 $\mu\text{g-at./liter}$ at 50 m. Maximum concentrations of about 50 $\mu\text{g-at./liter}$ were found at the same depth as the phosphate maximum.

The silicate concentration was about 3 $\mu\text{g-at./liter}$ at the surface and 20 $\mu\text{g-at./liter}$ at 50 m. Maximum observed silicate concentrations were about 100 $\mu\text{g-at./liter}$ at 1,000 m.

At 35 of the 50 stations in the dome, oxygen maxima and phosphate minima were found near the potential density surface $\sigma_t = 26.25$ g/liter (50 m in Fig. 3). Because the oxygen maxima and phosphate minima were not found at every station, and because double oxygen maxima were frequent, it is difficult to determine their origin. In the area of the dome, the oxygen maxima were always found between the

potential density surfaces $\sigma_t = 26.0$ and 26.5 g/liter, the layer in which Equatorial Subsurface Water is found. Bennett's (1963) chart of the oxygen distribution on the potential density surface $\sigma_t = 26.23$ g/liter ($\Delta t = 180$ cl/ton) shows an area of relatively high oxygen content that lies along the equator and spreads out toward the southeastern side of the Costa Rica Dome. The oxygen maximum in the Costa Rica Dome may be related to the presence of Equatorial Subsurface Water, water of high salinity that was formed south of the equator and subsequently modified by mixing in the Pacific Equatorial Undercurrent as it flowed northward across the equator.

HORIZONTAL DISTRIBUTION OF PROPERTIES

The distribution of salinity at the surface (Fig. 2b) shows low-salinity water (< 33‰) separating the high-salinity water in the Costa Rica Dome from the Central American coast. The occurrence of this low-salinity water was due to local coastal precipitation. Peterson (1960) has shown that during the rainy season, from May through November, the low-salinity water is confined to coastal areas near the Gulf of Nicoya, directly east of the dome. Thus, the low salinity observed at the eastern edge of the dome survey area was probably not representative of offshore surface conditions in the eastern tropical Pacific. Near Cocos Island to the south of the dome (Fig. 1), where coastal precipitation was not evident, the average surface salinity was 33.0‰. Maximum surface salinities (> 34‰) were found in the depression in dynamic topography along the 8th parallel and northward along the 88th meridian. These areas of high salinity indicate recently upwelled water. Southward flow along the 89th meridian, indicated by the dynamic topography (Fig. 2a), appears as an area of relatively low salinity.

The distribution of phosphate at the surface (Fig. 2d) was similar to that of salinity. The highest phosphate concentrations (> 0.9 $\mu\text{g-at./liter}$) were found in the depression in dynamic topography, and the lowest (< 0.5 $\mu\text{g-at./liter}$) were along the

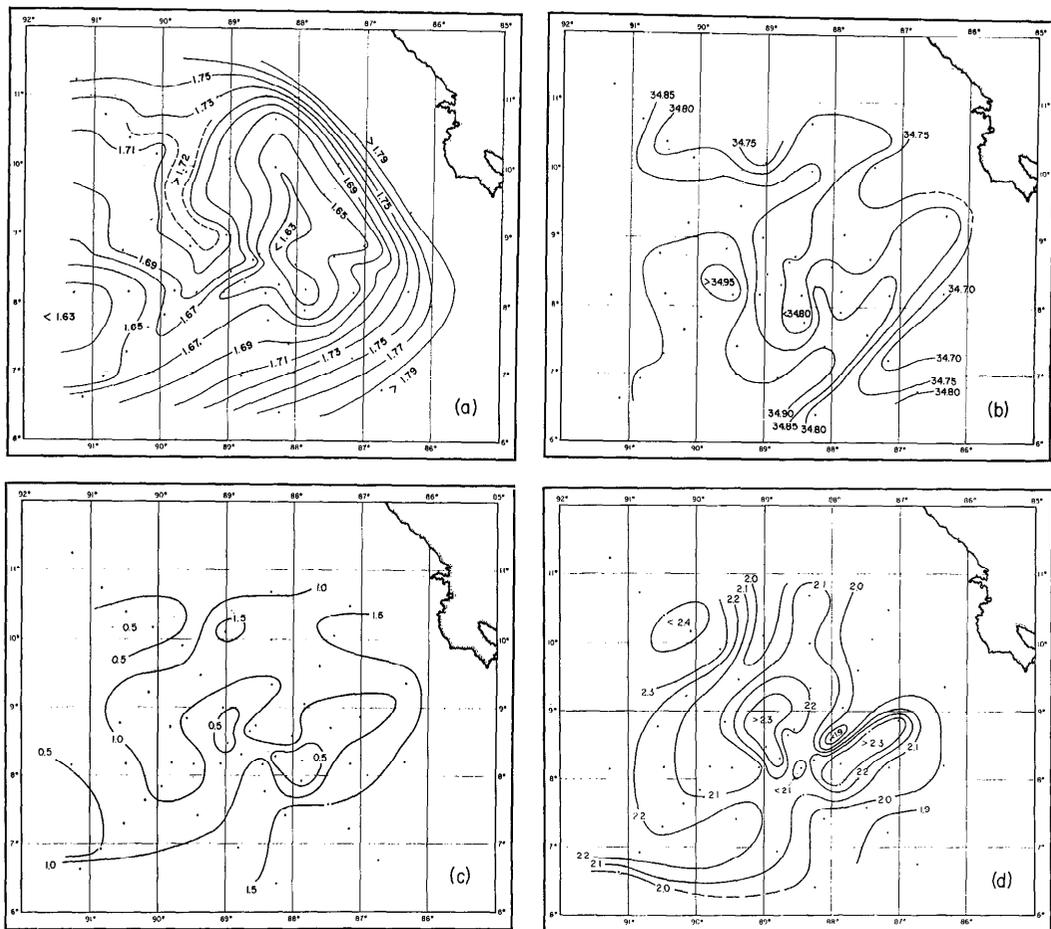


FIG. 4. Distribution of properties at 50 m during Costa Rica Dome cruise, November–December 1959: (a) Geopotential topography of the 50-decibar surface relative to 1,000 decibars, dynamic m; (b) 50-m salinity, ‰; (c) 50-m oxygen, ml/liter; (d) 50-m phosphate, $\mu\text{g-at./liter}$.

coast and in the low-salinity water along the 89th meridian. Near Cocos Island, phosphate concentrations were about $0.4 \mu\text{g-at./liter}$.

The oxygen distribution at the surface (Fig. 2c) was patchy and not clearly related to the circulation. At all stations in the dome, the surface water was undersaturated with oxygen. Surface concentrations ranged from 3.51 to 4.56 ml/liter (between 76.7 and 99.9% saturation). Lowest concentrations were observed near the phosphate and salinity maxima at 8°N lat, 88°W long. Near Cocos Island, surface oxygen contents were about 101% of the equilibrium solubility. At 50 m, the relation be-

tween circulation, salinity, oxygen, and phosphate may be clearly seen (Figs. 4a, b, c, d). At this depth, the salinity varied between 34.70 and 34.95‰ and was apparently little affected by coastal precipitation. Lowest oxygen concentrations (< 0.5 ml/liter) were coincident with highest phosphate concentrations ($> 2.2 \mu\text{g-at./liter}$). All the distributions show the influence of cyclonic circulation and upwelling.

The nitrate and silicate distributions were consistent with the phosphate and salinity distributions both at the surface and at 50 m. High nitrate and silicate concentrations were observed where salinity and phosphate contents were high. The horizontal distri-

butions of nitrate and silicate are not presented here, because these properties were observed at only one-third of the stations.

NUTRIENT RELATIONSHIPS

As organic matter is metabolized in the sea, organically bound phosphorus and nitrogen are returned to solution by bacterial oxidation. Simultaneously, dissolved oxygen is consumed (that is, the apparent oxygen utilization, or AOU, is increased). Upon complete oxidation of the organic matter, the phosphorus, nitrogen, and carbon that have been chemically combined in the organism are released into solution as inorganic phosphate, nitrate, and carbonate ions. The proportions in which they are released are determined by the proportions in which they were present in the living organism. Conversely, as phytoplankton synthesizes nutrients in the euphotic zone, inorganic phosphorus, nitrogen, and carbon become organically combined, and oxygen is produced as a by-product.

There is a growing body of evidence to suggest that oxygen, carbon, nitrogen, and phosphorus are assimilated and subsequently regenerated in the atomic ratios $-276 : 106 : 16 : 1$ (see Redfield, Ketchum, and Richards 1963). There are certain

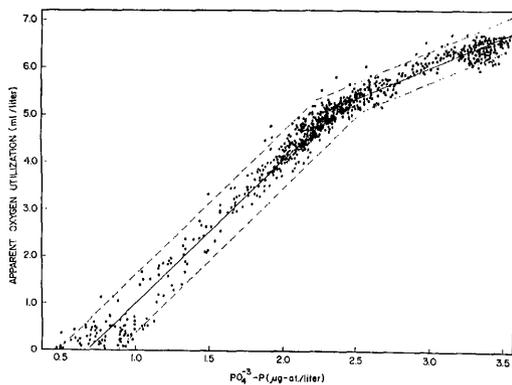


FIG. 5. Apparent oxygen utilization (AOU), ml/liter, vs. phosphate, $\mu\text{g-at./liter}$, in the Costa Rica Dome. The computed slopes are $\Delta\text{AOU}:\Delta\text{P} = 274:1$ by atoms for $\text{AOU} \leq 5.0$ ml/liter and $\Delta\text{AOU}:\Delta\text{P} = 114:1$ by atoms for $\text{AOU} > 5.0$ ml/liter. The dashed lines indicate the 95% confidence limits.

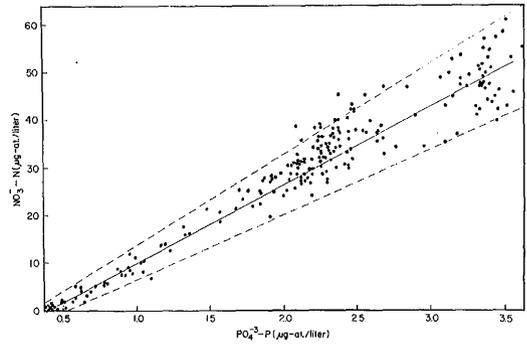


FIG. 6. Nitrate vs. phosphate, $\mu\text{g-at./liter}$, in the Costa Rica Dome. The computed slope is $\Delta\text{N}:\Delta\text{P} = 16.5:1$ by atoms. The dashed lines indicate the 95% confidence limits. The symbol \times represents the average surface value near Cocos Island that was not used in the regression analysis.

notable exceptions to this statistical relationship that will not be dealt with here.

In the Costa Rica Dome, the relationship between AOU and inorganic phosphate is not linear (Fig. 5). An abrupt change in slope is found near the value $\text{AOU} = 5.0$ ml/liter, $\text{PO}_4^{3-}\text{-P} = 2.3$ $\mu\text{g-at./liter}$. Two regression lines were computed for these data: the first for those values of $\text{AOU} \leq 5.0$ ml/liter, representing conditions in the water column above the potential density surface, where $\sigma_t = 26.3$ g/liter (above approximately 120 m), the second for values $\text{AOU} > 5.0$ ml/liter, representing conditions below $\sigma_t = 26.3$ g/liter (between about 120 and 1,100 m). The AOU-phosphate data do not appear to be linear for $\text{AOU} > 5.0$ ml/liter, but, for the purpose of demonstrating the differences above and below this value, a linear regression analysis was used for both groups of data.

The nitrate and phosphate data were separated into two groups whose corresponding AOU values were greater than and less than 5.0 ml/liter. The $\Delta\text{N}:\Delta\text{P}$ regression coefficients for these two groups were not significantly different, and it is concluded that the nitrate:phosphate ratio of change is constant throughout the water column (Fig. 6).

The AOU:phosphate ratio of change in the water above 120 m (that is, $\text{AOU} \leq$

TABLE 1. *Results of linear regression analyses*

Apparent oxygen utilization vs. inorganic phosphate						
Range	b (ml/ μ g-at.)	$S_{y x}$ (ml/liter)	S_b (ml/ μ g-at.)	r	n	$\Delta\text{AOU} : \Delta\text{P}$ (atom : atom)
AOU \leq 5.0 ml/liter ($\sigma_t \leq$ 26.3 g/liter)	3.07	± 0.31	± 0.03	+0.98	420	274 : 1
AOU > 5.0 ml/liter ($\sigma_t >$ 26.3 g/liter)	1.28	± 0.16	± 0.02	+0.96	450	114 : 1

Inorganic nitrate vs. inorganic phosphate						
Range	b (atom : atom)	$S_{y x}$ (μ g-at./liter)	S_b (atom : atom)	r	n	$\Delta\text{N} : \Delta\text{P}$ (atom : atom)
All data	16.5	± 2 ($x = 1.0$) ± 5 ($x = 3.5$)	± 0.45	+0.95	200	16.5 : 1

5.0 ml/liter) (Table 1) is in excellent agreement with the normal oxidative ratio $\Delta\text{AOU} : \Delta\text{P} = 276 : 1$ proposed by other authors (Redfield et al. 1963). Because oxygen may be transferred across the sea surface, the $\Delta\text{AOU} : \Delta\text{P}$ relation computed from data obtained from the surface layer might not necessarily represent the true oxidative ratio. However, as will be shown in the next section, the addition of oxygen from the surface is probably important only to depths of 20 m. Because the data obtained from the surface to 20 m do not appear to deviate from the regression line established by data collected between 20 and 120 m (Fig. 5), it is probable that the regression line does represent the AOU : phosphate oxidative ratio which has the value $274 : 1 \pm 5$ at the 95% confidence level.

The $\Delta\text{AOU} : \Delta\text{P}$ ratio computed for data collected below 120 m (Table 1) (that is, AOU > 5.0 ml/liter) is less than half the normal oxidative ratio. This low ratio can be explained in terms of the preformed phosphate distribution. In the Costa Rica Dome, the preformed phosphate content (that amount of phosphate that has not been derived from the decomposition of organic material but was present in the dissolved inorganic form when the water sank below the surface) is constant (about 0.65 μ g-at./liter) from the sea surface to the potential density surface $\sigma_t = 26.3$ g/liter, the density level at which the change in slope occurs. The depth at which the slope changes varies from place to place

but is approximately 120 m. Between this level and the maximum sampling depth, where $\sigma_t = 27.4$ g/liter, the preformed phosphate content increases from 0.65 to 1.25 μ g-at./liter. It is likely, although not conclusive, that the AOU : phosphate ratio observed below the level $\sigma_t = 26.3$ g/liter results from a mixture of Equatorial Subsurface Water containing little preformed phosphate and intermediate water containing large amounts of preformed phosphate, rather than from a change in the oxidative ratio. The mixture of these two waters containing different amounts of preformed phosphate need not produce a linear AOU : phosphate relationship. This hypothesis is consistent with Redfield's (1942) explanation of the phosphate distribution in the Atlantic Ocean, in which he demonstrated that large amounts of preformed phosphate spread out isentropically from the Antarctic Convergence toward the equator between the levels $\sigma_t = 27.2$ and 27.6 g/liter.

The nitrate : phosphate ratio of change is $16.5 : 1 \pm 0.9$ at the 95% confidence level, in agreement with the previously established value of 16 : 1. The fact that the slope $\Delta\text{N} : \Delta\text{P}$ is constant over the complete range of observed values is evidence that the change in slope in the AOU : phosphate relationship is caused by inequalities in the preformed phosphate distribution. The absence of a break in slope in the nitrate : phosphate relationship suggests that the amounts of preformed nitrate and

performed phosphate are equivalent throughout the water column and that the oxidative ratios do not vary.

THE OXYGEN MODEL

The distribution of oxygen in the sea is determined by a complicated interplay of physical and biological processes. Richards (1957) has reviewed these processes. They are: 1) photosynthetic production in the euphotic zone, 2) atmospheric exchange (gain or loss) at the sea surface, 3) respiratory consumption at all depths, and 4) circulatory and mixing processes. An attempt will be made to estimate the magnitude of these processes in the near-surface layer of the Costa Rica Dome through the use of a simple model.

In this model, the dome is considered to be an area where water of uniform high salinity, high phosphate, and low oxygen concentrations is brought close to the surface by upwelling from some depth d . Surface water in the area close to, but uninfluenced by, the dome is assumed to have uniform low salinity, low phosphate, and high oxygen contents. Mixing of these two water types is assumed, so that the fraction of each water type in the mixture is a linear function of salinity. Thus,

$$P_{\text{mixing}} = P_a \frac{(S - S_0)}{(S_a - S_0)} + P_0 \frac{(S_a - S)}{(S_a - S_0)}, \quad (1)$$

where P_{mixing} is the phosphate content due to mixing in the absence of biological processes, P_a the phosphate content characteristic of the water type at depth d , P_0 the phosphate content of the surface water type, S_a the salinity of the deep water, S_0 the salinity of the surface water, and S the observed salinity at each sampling depth.

Similarly, the oxygen content due to mixing can be computed as

$$O_{\text{mixing}} = O_a \frac{(S - S_0)}{(S_a - S_0)} + O_0 \frac{(S_a - S)}{(S_a - S_0)}, \quad (2)$$

where O_{mixing} is the oxygen concentration that would result from the mixture of these two water types in the absence of atmospheric exchange and biological processes,

O_d the oxygen content of the deep water type, and O_0 the oxygen content of the surface water type.

The effect of biological production (or consumption) of oxygen can be estimated from the difference between the observed phosphate concentration and the phosphate concentration computed for the mixture. Thus, the net amount of oxygen produced biologically at each sampling depth would be

$$O_{\text{biol}} = (P - P_{\text{mixing}}) \Delta O : \Delta P, \quad (3)$$

where O_{biol} is the amount of oxygen produced (or consumed, if the value is negative), P the observed phosphate concentration, and $\Delta O : \Delta P$ the ratio of change relating the production of oxygen to the consumption of phosphate.

If the Costa Rica Dome can be considered to be a two-component system, and if the biological production is estimated by equation (3), the oxygen concentration at any depth above d is

$$O_{\text{model}} = O_{\text{mixing}} + O_{\text{biol}}, \quad (4)$$

so that O_{model} is a function of salinity and phosphate.

The boundary conditions, which are the salinity, phosphate content, and oxygen content of the unmixed deep and surface components, must be chosen to represent average values of these water types.

The salinity maximum, as determined by averaging the station data by depth, is found at 105 m. This is the greatest depth at which the model would be valid, because it is assumed that the salinity above the lower boundary is always less than the salinity at this boundary. Because productivity measurements indicate negligible net production below 50 m, the lower boundary is set at 65 m, which is the next lower sampling depth. Limiting the model to 65 m rather than to 105 m reduces the possible effects of lateral mixing processes that are unaccounted for by the model. The boundary conditions determined by averaging the station data at 65 m and their respective standard deviations from the mean are: $S_a = 34.85\% \pm 0.05\%$, $P_a = 2.13 \mu\text{g-at./}$

TABLE 2. Average observed and computed distributions of oxygen in the Costa Rica Dome*

Depth (m)	Observed oxygen (ml/liter)	Computed oxygen (ml/liter)	Produced biologically in ml/liter (%)	Mixed from surface in ml/liter (%)	Upwelled from depth in ml/liter (%)	Model anomaly in ml/liter (%)
0	4.19	3.91	0.60 (15)	3.01 (77)	0.30 (8)	+0.28 (7)
10	3.72	3.59	0.86 (24)	2.24 (62)	0.49 (14)	+0.13 (4)
20	2.22	2.37	0.87 (37)	0.70 (29)	0.80 (34)	-0.15 (6)
30	1.56	1.60	0.49 (31)	0.19 (12)	0.92 (57)	-0.04 (2)
40	1.19	1.22	0.22 (18)	0.05 (4)	0.95 (78)	-0.03 (2)
50	1.04	1.01	0.03 (3)	0.02 (2)	0.96 (95)	+0.03 (3)
65	0.96	0.99	0.03 (3)	0.00 (0)	0.96 (97)	-0.03 (3)

* This table gives the average results of computations using the oxygen model described in the text. Each value represents data from 50 stations. The computed oxygen concentrations are the sums of contributions from biological production (equation [3]) and from oxygen originally present in the two water components (equation [2]); the model anomaly is the difference between the observed and computed oxygen contents. The numbers in parentheses are the percentages of the computed total oxygen content at the corresponding depths.

liter $\pm 0.14 \mu\text{g-at./liter}$, $O_d = 0.96 \text{ ml/liter} \pm 0.32 \text{ ml/liter}$.

The salinity, phosphate, and oxygen contents of the surface water component were taken from the values observed around Cocos Island (Fig. 1). These averages and their standard deviations computed from 48 observations near the island are: $S_0 = 33.00\text{‰} \pm 0.05\text{‰}$, $P_0 = 0.41 \mu\text{g-at./liter} \pm 0.04 \mu\text{g-at./liter}$, and $O_0 = 4.57 \text{ ml/liter} \pm 0.18 \text{ ml/liter}$ (101% of saturation). Bennett's (1963) surface salinity chart shows that surface conditions near Cocos Island are representative of the area south of the Costa Rica Dome and that the surface properties near the island are probably not greatly influenced by the dome. Cocos Island lies in the path of the North Equatorial Counter-current, and surface water near the island is probably representative of water that is mixed into the upwelling region. The low-salinity water near the coast is assumed to be confined to coastal areas and not to play an important role in the mixing process.

The oxidative ratio $\Delta O : \Delta P$ is taken as $-276 : 1$ by atoms or $-3.09 : 1 \text{ ml O}_2 : \mu\text{g-at. PO}_4^{3-}\text{-P}$, which is the normal value proposed by Redfield et al. (1963). The use of this value is justified on the basis of the $\Delta\text{AOU} : \Delta P$ ratio computed statistically from observed data.

RESULTS OF THE OXYGEN MODEL

The oxygen model was used to compute the vertical distribution of oxygen at the 50 stations occupied during the Costa Rica Dome cruise. The average results of these calculations (Table 2) are separated into three components: a) oxygen produced biologically, b) oxygen mixed into the dome with surface water, and c) oxygen originally present in the deep water that upwelled from depth. Component a) was computed from equation (3), while b) and c) were computed from the two terms in equation (2).

The vertical distribution of oxygen produced by photosynthesis and that of the incubator productivity are similar in shape (Fig. 7), and although the maximum in the distribution of oxygen due to biological production coincides with the maximum in productivity, these maxima result from different processes. This is readily seen from the following argument.

If there were no mixing, and if upwelling brought undiluted deep water directly to the surface, the oxygen content due to biological production would increase from zero at the compensation depth to a maximum at the surface. That is, as water ascends through the euphotic zone, oxygen accumulates owing to photosynthetic production. The distribution of oxygen resulting from this process alone would, in effect, be proportional to the integral of the productivity distribution from the compensation depth to the depth in question. The effect of mixing surface water with deep water, as assumed in the model, can be compensated for by dividing the oxygen content due to biological production by the fraction of deep water at each depth. The amount of oxygen produced biologically in a unit volume of upwelled deep water is estimated in

this way. The distribution of oxygen produced biologically in a unit volume of deep water (Fig. 7) shows that this quantity is nearly zero at 65 m, increases to a maximum value at the surface, and exhibits its maximum gradient at the depth of the productivity maximum. Therefore, the distribution of oxygen produced per unit volume of deep water is consistent with the productivity distribution, and the similar shapes of the biological oxygen curve as estimated from the model and the distribution of productivity are a consequence of the mixing processes. The subsurface productivity maximum is generally attributed to light inhibition at the surface.

If the model accurately describes the net biological production of oxygen, these values should agree with productivity measurements. Integrating the oxygen content resulting from biological production from 65 m to the surface gives 2.9×10^4 ml O_2/m^2 . If the ratio of oxygen production to carbon assimilation by atoms is $\Delta O : \Delta C = -276 : 106$, the net amount of carbon fixed would be 1.2×10^4 mg C/ m^2 . Under the assumptions of the model, it is estimated that 87% of the water above 65 m has been upwelled at a velocity of 10^{-6} m/sec (Wyrki 1964). Therefore, the net productivity estimated from the model is 190 mg C m^{-2} day $^{-1}$, which agrees well with *in situ* productivity measurements of between 160 and 440 mg C m^{-2} day $^{-1}$.

The distributions of oxygen derived from the surface and deep water components (Table 2) are inversely related. At the surface, 77% of the oxygen content originated in what is assumed to be surface water like that observed near Cocos Island, and only 8% was upwelled from depth. At 50 m, there is a 2% contribution from the surface and a 95% contribution from deep water. Between 10 and 50 m, the distribution of oxygen that has been mixed into the water column with surface water is exponential (Fig. 8). Broenkow and Bennett (unpublished data) have shown that an exponential distribution could be expected in a two-component system with upwelling, and the observed distribution supports the assumed

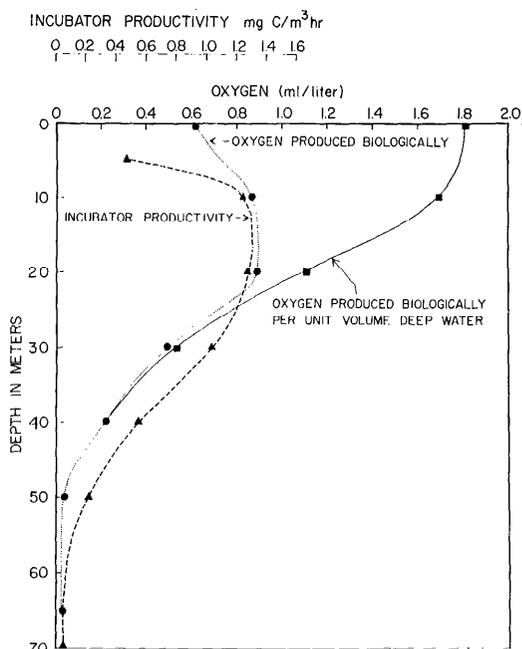


FIG. 7. Average vertical distributions of oxygen produced biologically computed from the model and oxygen produced biologically per unit volume of deep water, ml/liter; average vertical distribution of incubator productivity from 11 stations in the Costa Rica Dome, mg C m^{-3} hr $^{-1}$. The amount of oxygen produced biologically per unit volume of deep water is the amount of oxygen produced biologically at each depth divided by the fraction of deep water at that depth.

mixing process. It should be repeated for the sake of clarity that the computed distributions of oxygen mixed from the surface and deep water components are merely functions of salinity (*see equation [2]*).

The distribution of the model anomaly, which is the difference between the observed and computed oxygen concentrations, shows the effect of oxygen exchange with the atmosphere (Table 2). Because the model does not allow for exchange of oxygen across the sea surface, these effects can be deduced only from the model anomaly. At the surface and at 10 m, the observed oxygen content is greater than that computed from the model by 7 and 4% of the computed contents at those depths. Because the surface layer in the Costa Rica Dome is everywhere undersaturated with

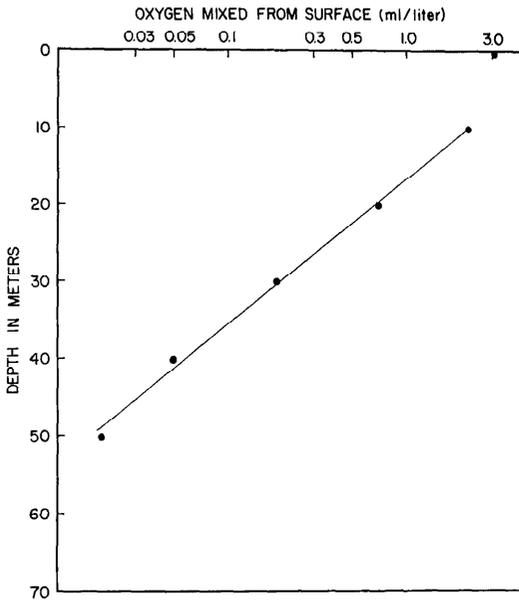


FIG. 8. Average vertical distribution of oxygen, computed from the model, that has been mixed into the water column with surface water, ml/liter, logarithmic plot.

oxygen (Fig. 2c), it is likely that these anomalies result from a net transport of oxygen into the sea. The anomalies between the surface and 20 m are significant at the 95% confidence level. Below 20 m, the differences between the model and observations are not significant at the 95% level. The standard error of estimate of the model anomaly is constant with depth and is ± 0.3 ml O_2 /liter.

THE NUTRIENT MODEL

A model similar to the oxygen model can be applied to the nitrate and silicate distributions. The assumptions involved in the oxygen model also apply to the nutrient model. Because the nitrate and silicate contents in the surface water near Cocos Island are negligible, nutrient models analogous to equation (4) become

$$N_{\text{model}} = N_a \frac{(S - S_0)}{(S_a - S_0)} + (P - P_{\text{mixing}}) \Delta N : \Delta P \quad (5)$$

and

$$Si_{\text{model}} = Si_a \frac{(S - S_0)}{(S_a - S_0)} + (P - P_{\text{mixing}}) \Delta Si : \Delta P, \quad (6)$$

where N_{model} and Si_{model} are the nitrate and silicate contents computed from the model. N_a and Si_a are the nitrate and silicate concentrations at $d = 65$ m and equal $29.3 \mu\text{g-at. NO}_3^- \text{-N/liter}$ and $21.0 \mu\text{g-at. SiO}_4^{4-} \text{-Si/liter}$. $\Delta N : \Delta P$ and $\Delta Si : \Delta P$ are the assimilation ratios of change that relate nitrate and silicate consumption to the phosphate consumption.

The ratio of change $\Delta N : \Delta P$ is well known and has been estimated by numerous authors to be between 15 : 1 and 16 : 1 (Redfield et al. 1963). The value $\Delta N : \Delta P = 16 : 1$ was used in these computations and is within the range computed statistically (Table 1). There is, however, no universal regeneration or assimilation ratio that can be used in the silicate model. The analysis of plankton gives Si : P concentration ratios varying between 16 : 1 and 50 : 1 (Vinoogradov 1953). Richards (1958) found the ratio of change $\Delta Si : \Delta P = 15 : 1$ for waters of the western Atlantic, and Stefánsson and Richards (1963) found the ratio of change $\Delta Si : \Delta P = 22 : 1$ in the eastern North Pacific.

Assuming that the model can be used to describe the silicate distribution, the silicate content calculated from the model should equal the observed silicate concentration, and equation (6) can then be rewritten

$$\Delta Si : \Delta P = \frac{Si_a \frac{(S - S_0)}{(S_a - S_0)} - Si}{P_a \frac{(S - S_0)}{(S_a - S_0)} + P_0 \frac{(S_a - S)}{(S_a - S_0)} - P}, \quad (7)$$

where Si refers to the observed silicate concentrations. The numerator of equation (7) is termed the "silicate anomaly" after Stefánsson and Richards (1963), and the denominator is termed the "phosphate anomaly." The regression coefficient of the numerator on the denominator is the silicate : phosphate ratio of change.

The nitrate concentrations computed from the model agree with observations (Fig. 9). The regression coefficient of the computed vs. the observed data is +0.97, which is not significantly different from

1.0. This suggests that the assumed assimilation ratio, $\Delta N : \Delta P = 16 : 1$, applies and also that the nutrient model could be used to estimate the $\Delta Si : \Delta P$ ratio of change.

The regression line (Fig. 10) computed to determine the ratio of change $\Delta Si : \Delta P$ (based on 91 samples) is

$$\text{silicate anomaly} = 0.7 + 16.2 \times \text{phosphate anomaly},$$

where the silicate anomaly is the numerator and the phosphate anomaly the denominator in equation (7). The ratio of change expressed by atoms is

$$\Delta Si : \Delta P = 16.2 : 1 \pm 1.6 \text{ (at the 95\% confidence level).}$$

The fact that the regression line does not pass through the origin is probably due to small inaccuracies in the boundary conditions.

CONCLUSIONS

The distributions of the nutrients and oxygen in the Costa Rica Dome are determined mainly by the localized upwelling of nutrient-rich, oxygen-poor water from 65 m or deeper and its subsequent mixing with surface water having high oxygen and low nutrient contents. As the water ascends

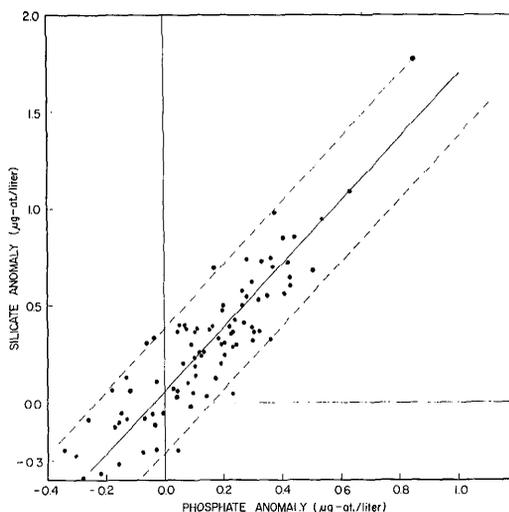


FIG. 10. Silicate anomaly vs. phosphate anomaly, $\mu\text{g-at./liter}$. The anomalies are the differences between the observed silicate and phosphate concentrations and those computed for a mixture of deep and surface waters (equation [7]). Computed slope is $\Delta Si : \Delta P = 16.2 : 1$. Dashed lines indicate 95% confidence limits.

through the euphotic zone, the distributions of these chemical properties are further modified by biological consumption of nutrients.

Assuming that the surface layer of the Costa Rica Dome is a two-component mixture of water upwelled from 65 m and surface water, and that the proportions of water from each of these sources can be estimated from the observed salinity, the distribution of oxygen was estimated on the basis of the phosphate content. The average computed oxygen distribution agrees well with the average observed distribution except at the surface, where the atmospheric exchange of oxygen is important. The gross oxygen budget above 65 m is estimated as: 38% of the oxygen content was present in the deep water before upwelling, 37% was present in the surface water and was mixed into the dome, 22% was biologically produced *in situ*, and 3% entered the sea by atmospheric exchange.

The average rate of carbon fixation based on the model is about $190 \text{ mg C m}^{-2} \text{ day}^{-1}$. As much as $10 \mu\text{g-at./liter}$ of silicate-silicon, $10 \mu\text{g-at./liter}$ nitrate-nitrogen, and $0.6 \mu\text{g-}$

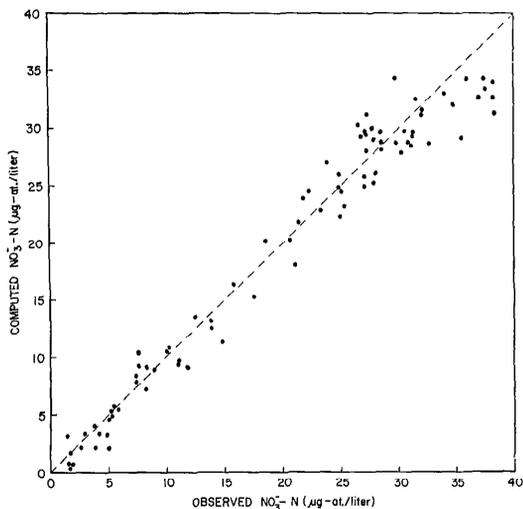


FIG. 9. Nitrate content computed from model vs. observed nitrate, $\mu\text{g-at./liter}$. Dashed line indicates 1:1 correlation.

at./liter of phosphate-phosphorus were consumed by photosynthetic activity in the dome as the water was upwelled. Silicate, nitrate, and phosphate appear to be biologically utilized in the atomic ratio 16 : 16 : 1.

The ratio of change $\Delta\text{AOU} : \Delta\text{P}$ as computed by regression analysis is not constant in the dome. An abrupt change in the ratio is found at the potential density surface $\sigma_t = 26.3$ g/liter. Above this surface ($\text{AOU} \leq 5.0$ ml/liter), the atomic ratio of change is $\Delta\text{AOU} : \Delta\text{P} = 274 : 1$, and below this surface ($\text{AOU} > 5.0$ ml/liter) the ratio is $\Delta\text{AOU} : \Delta\text{P} = 114 : 1$. The change in slope is thought to be due to an increasing amount of preformed phosphate below the surface $\sigma_t = 26.3$ g/liter. The $\Delta N : \Delta P$ ratio of change is 16.5 : 1 and is constant over the concentration range observed in the dome.

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