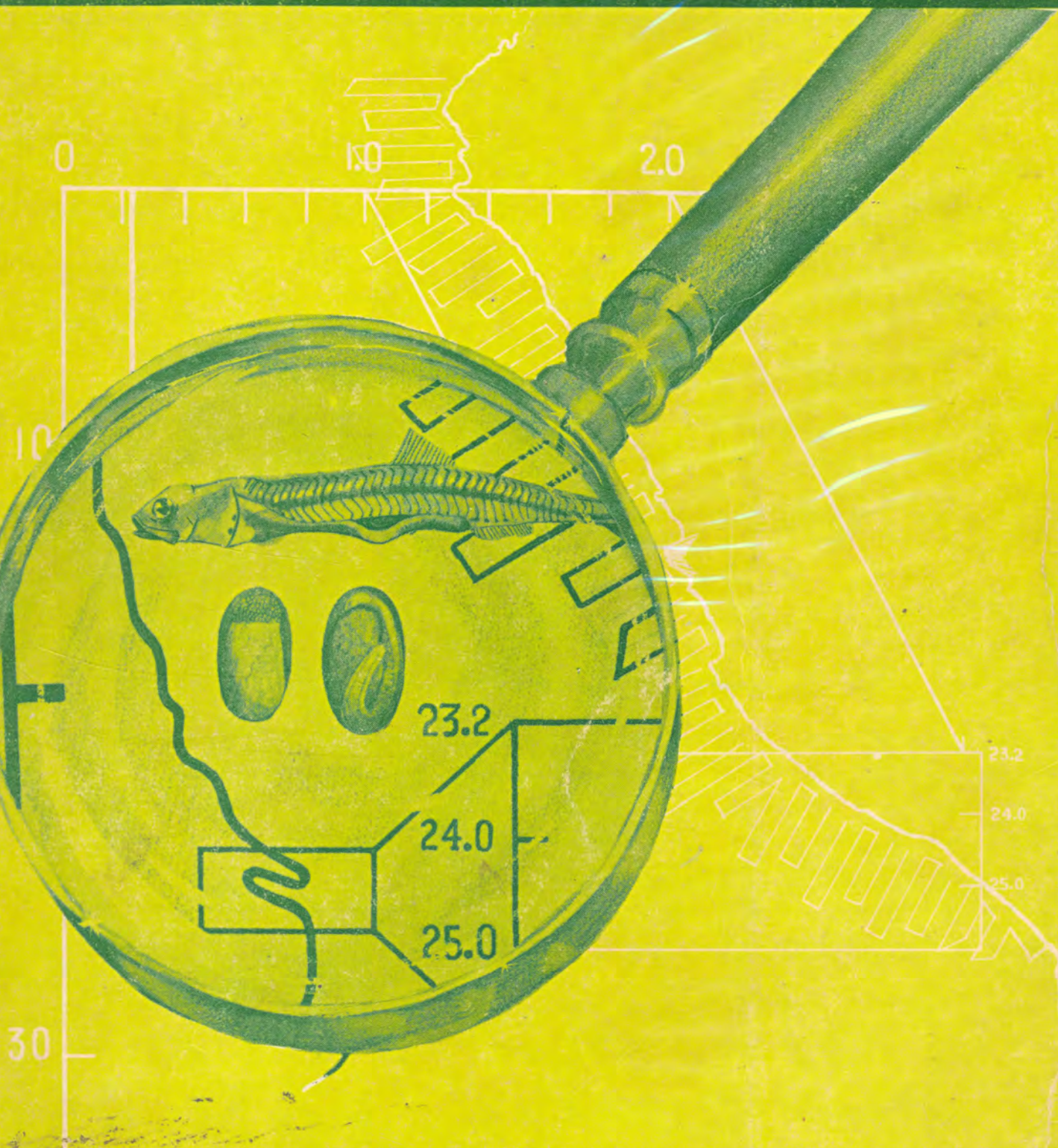




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**INVESTIGACION COOPERATIVA DE LA ANCHOVETA
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PRIMARY PRODUCTION AND NUTRIENT FLUXES OFF THE NORTHERN COAST OF PERU: A SUMMARY

by

Glen Harrison and Trevor Platt

Fisheries and Oceans
Marine Ecology Laboratory
Bedford Institute of Oceanography
Dartmouth, N. S.
Canada B2Y 4A2

ABSTRACT

The distribution and magnitude of primary production measured during the 1977 ICANE cruise off the northern coast of Peru (9°S Lat.) were generally comparable to levels further south (15°S Lat.). Daily production rates in excess of $5 \text{ g C m}^{-2} \text{ d}^{-1}$ were common within 10 km of shore but were highly variable in space and time. Nitrogen and phosphorus assimilation showed a similar distribution. Phytoplankton cellular compositional ratios and nutrient assimilation ratios (C:N:P) were generally higher than the "Redfield ratio" (106:16:1) at the productive inshore stations and lower offshore. High C:N assimilation ratios in near surface waters and euphotic zone NO_3 versus SiO_3 plots suggested nitrogen limitation of primary production.

RESUMEN

Durante el crucero de ICANE de 1977 frente a la costa norte del Perú (9°S) la magnitud y distribución de la producción primaria fueron en general comparables con las observadas en el sur (15°S). Las tasas de producción mayores de $5 \text{ g Cm}^{-2} \text{ d}^{-1}$ fueron corrientes dentro de los 10 Km cercanos a la a la costa pero con una distribución espacio-temporal muy variable. La asimilación de fósforo y de nitrógeno se distribuyó en forma similar. Las proporciones de la composición del fitoplancton celular así como las de asimilación de nutrientes (C:N:P) fueron en general más altas que las "proporciones de Redfield" (106:16:1) en las estaciones cercanas y medianamente alejadas de la costa en que hubo producción. La alta relación C:N cerca de la superficie así como el ploteo de NO_3 contra Si O_3 en la zona eufótica sugieren que la producción primaria puede estar limitada por el nitrógeno.

INTRODUCTION

The persistence of highly productive waters off the coast of Peru is a consequence of continuous upwelling of nutrient-rich subsurface waters. Inorganic nutrients (NO_3 , SiO_3 , PO_4) may be most important in regulating the observed high rates of production and high yields of phytoplankton biomass in this region. During the 1977 ICANE cruise, we studied the distribution, availability and utilization of inorganic nitrogen (NO_3 , NH_3) and phosphorus (PO_4) in relation to standard surveys of primary production (carbon fixation) off the northern coast of Peru.

METHODS

Photosynthesis (carbon-14 uptake), $^{15}\text{NO}_3$ and $^{15}\text{NH}_4$ assimilation, and $^{33}\text{PO}_4$ assimilation measurements were made on samples collected from 100%, 50%, 25%, 10%, 5% and 1% light penetration depths. Tracer experiments followed essentially the methods outline in Strickland and Parsons (1972) for carbon-14, Dugdale and Goering (1967) for nitrogen-15 and Harrison et al. (1977) for phosphorus-33. Samples were incubated for 24 hrs in simulated *in situ* deck incubators cooled with near-surface seawater. Supporting data (e.g., nutrient concentrations,

particulates, etc.) and analytical procedures are presented in the ICANE data report (Doe, 1978). Station locations are presented in Figs. 1 and 2.

RESULTS AND DISCUSSION

1. Primary Production.— Photosynthetic rates ranged from 0.3 to 15.3 g C m⁻² d⁻¹ (\bar{x} = 4.3). Highest values were found inshore (within 5 km) and lowest values offshore (180 km). Maximum production rates were generally found at the surface. Production (m⁻²) decreased with increased euphotic depth (Fig. 3) and depth of the nutricline (Fig. 4). Inshore, 75 to 85% of the phytoplankton biomass and photosynthetic activity was associated with particles retained on a 35 μ nitex net (Table 1). In one experiment, more than 40% were retained on a 202 μ net. Estimates of phytoplankton growth rates from C-14 data (using a C/Chl ratio of 62, Fig. 5) averaged 0.52 doublings d⁻¹ for STN 71-222 and 0.72 for STN 193-336.

2. Nutrient Concentrations.— Stations were grouped according to their euphotic zone nutrient distributions (Fig. 6). Some inshore stations (56, 75, 84) exhibited high nutrient (NO₃, SiO₃, PO₄) concentrations at the surface and a shallow (<10m) nutricline. Another group (STN 193, 197, 222) further offshore, exhibited lower nutrient concentrations at the surface and a deeper (>10m) nutricline. A final inshore group (STN 71, 95) showed low NO₃ levels and extremely high SiO₃ and PO₄ values. Station 204 (*M. rubrum* station) was included in this group for its extremely low values of all nutrients. Nitrate - PO₄ plots of all stations revealed a linear relationship (slope ~12) with a PO₄ intercept (Fig. 7). The NO₃ - SiO₃ plot was non-linear with a slight SiO₃ intercept (Fig. 8). Based on these distributions, euphotic zone nutrient concentrations were related to station productivity. Inshore, productive stations were depleted in NO₃

and high in regenerated nutrients (SiO₃, PO₄, and NH₃, Fig. 9). Inshore stations with high NO₃ concentrations were probably in early stages of the upwelling-production cycle. It appeared that as phytoplankton biomass increase, NO₃ was depleted relative to SiO₃ and PO₄ and at the extreme, large amounts of SiO₃, PO₄ and NH₃ were regenerated at the shallow inshore stations overlying anoxic bottom waters. In addition, presence of significant concentrations of regenerated nutrients in the surface at inshore stations suggested entrainment by the upwelling process.

Table 1. Size fractionation of phytoplankton, Peru 1977. Particulates: CHL = chlorophyll (mg m⁻³); POC, PON = particulate organic carbon and nitrogen, respectively (mg m⁻³). Productivities: CO₂ = photosynthetic carbon fixation (mg C m⁻² d⁻¹); NO₃, NH₃ and PO₄ = mg-at m⁻² d⁻¹. Regeneration: PO₄ = mg-at m⁻² d⁻¹. Numbers in parentheses are percentages of total.

Stn 133 (8°51.3'S, 78°51.3'W) surface				
A. Particulates	>202 μ	35-202 μ	1-35 μ	<1 μ
Chl	0.41(46)	0.34(38)	0.13(14)	0.02(2)
B. Productivities				
CO ₂	180.4(40)	216.3(48)	37.2(8)	15.8(4)
CO ₂ (Dark)	1.7(16)	0.1(1)	3.4(31)	5.8(53)
NO ₃	0.149(52)	0.107(38)	0.025(9)	0.002(1)
NH ₃	0.140(39)	0.167(47)	0.046(13)	0.005(1)
PO ₄	0.047(27)	0.088(51)	0.023(13)	0.014(8)
Stn 251(9°12.6'S, 78°37.7'W) surface				
A. Particulates	>202 μ	35-202 μ	1-35 μ	<1 μ
Chl	n.d.(0)	5.31(74)	0.73(10)	1.15(16)
POC	23(3)	387(52)	227(31)	104(14)
PON	11(8)	98(66)	17(11)	23(15)
B. Productivities				
CO ₂	n.d.(0)	589.8(85)	68.6(10)	35.5(5)
NH ₃	n.d.(0)	0.263(41)	0.101(16)	0.271(43)
PO ₄	n.d.(0)	0.188(72)	0.036(14)	0.037(14)
C. Regeneration				
PO ₄	n.d.(0)	0.050(26)	0.144(74)	n.d.(0)

Fig. 1. Station locations, 1977 ICANE cruise.

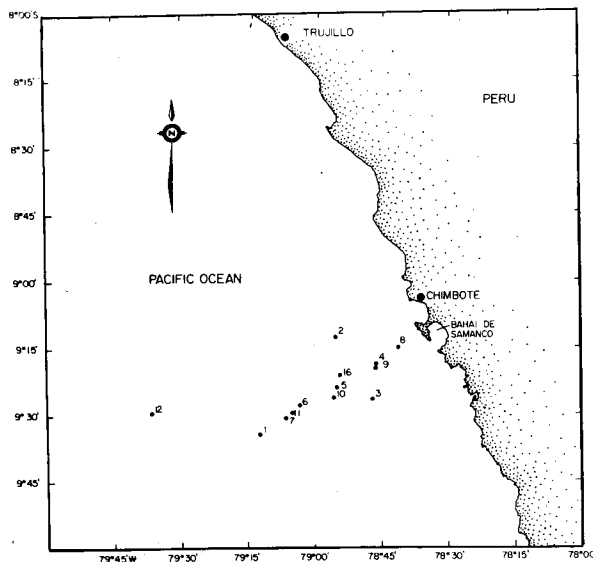
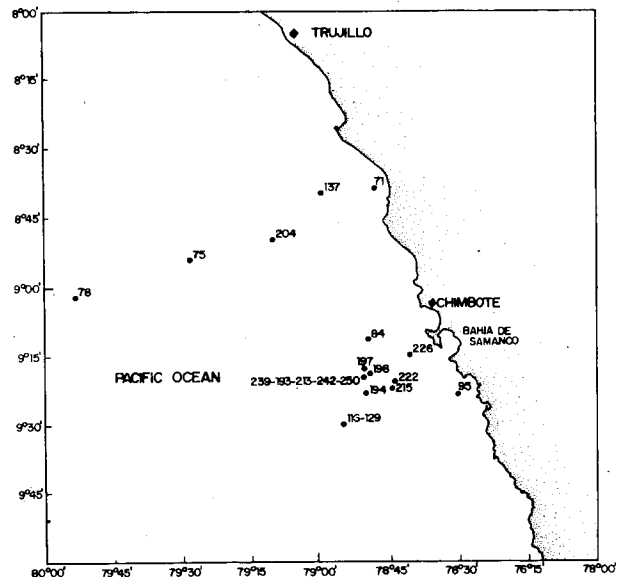


Fig. 2. Detailed station locations off the Peru coast.



3. Nitrogen Assimilation – Nitrogen ($\text{NO}_3 + \text{NH}_3$) assimilation averaged $20.1 \text{ mg-atoms m}^{-2} \text{ d}^{-1}$ (Table 2): 66% was attributed to NO_3 assimilation alone (Table 3). However, at the productive inshore stations (e.g., STN 71) as much as 90% of the nitrogen assimilated was in the form of NH_3 . Also, relatively more NH_3 was assimilated by the smaller size fractions of the populations (ref. Table 1). Nitrate turnover times for all stations averaged 10.6 days but was quite variable. On the other hand, NH_3 turnover averaged only 3.0 days and was relatively invariant. Carbon:

nitrogen ($\text{NO}_3 + \text{NH}_3$) assimilation ratios, which averaged 7.7 (Table 2), were much more variable than C:N particulate compositional ratios (Fig. 10) but were positively related (Fig. 11). Assimilation

Fig. 3. Relationship between primary production and depth of the euphotic zone.

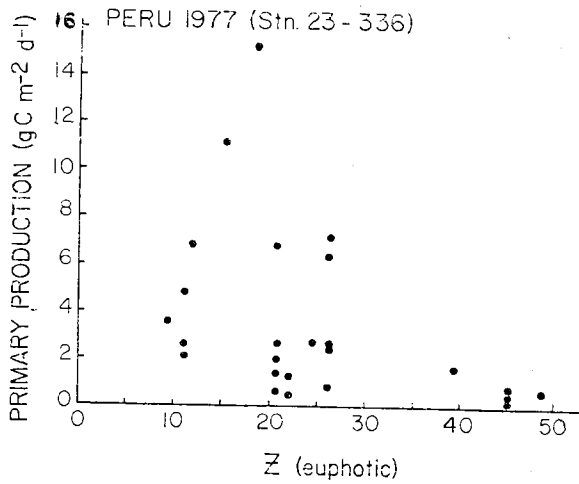


Fig. 4. Relationship between carbon and nitrate productivities and depth of the nutricline. Open triangles represent stations where nitrate concentrations were low at all euphotic depths.

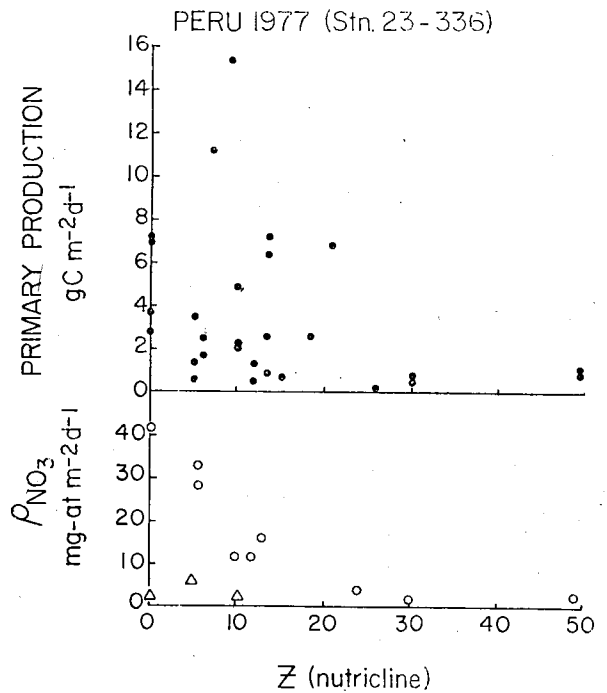


Table 2. Carbon, nitrogen and phosphorus productivities, Peru 1977.

Stn.	Lat.	Photosynthesis $\text{g C m}^{-2} \text{ d}^{-1}$	N-assimilation P-assimilation $(\text{mg-at m}^{-2} \text{ d}^{-1})$		C:N:P (atomic)
23	5°04'N	1.076	12.459	4.636	19: 3:1
37	0°42'N	0.726	6.669	1.897	32: 4:1
48	3°07'S	0.790	11.716	1.796	37: 7:1
56	6°47'S	2.585	57.688	2.168	99:27:1
71	8°40'S	6.990	26.079	4.171	140: 6:1
75	8°54'S	1.729	31.948	1.601	90:20:1
84	9°12'S	2.659	35.363	1.779	125:20:1
95	9°23'S	3.661	8.519	1.774	172: 5:1
193	9°20'S	0.515	15.491	0.869	49:13:1
197	9°20'S	0.637	13.969	1.109	48:13:1
204	8°50'S	2.011	5.035	0.952	176: 5:1
222	9°22'S	<u>0.897</u>	<u>24.582</u>	<u>1.160</u>	<u>64:21:1</u>
$\bar{x}(71-222)$		2.387	20.123	1.677	108:14:1

ratios were generally higher than the Redfield ratio (C:N = 6.6:1) inshore and lower offshore.

4. Phosphorus Assimilation.— Phosphate assimilation rates averaged $1.68 \text{ mg-atoms m}^{-2}\text{d}^{-1}$ (Table 2). Carbon: phosphorus assimilation ratios averaged 108:1 and N:P ratios averaged 14:1, not significantly different from the Redfield compositional ratio. Station-to-station C:P assimilation ratios varied significantly and were positively associated with phytoplankton biomass (Fig. 12). That is to say, C:P assimilation ratios, as C:N ratios, were

Fig. 5. Relationship between particulate organic carbon (POC) and chlorophyll (Chl).

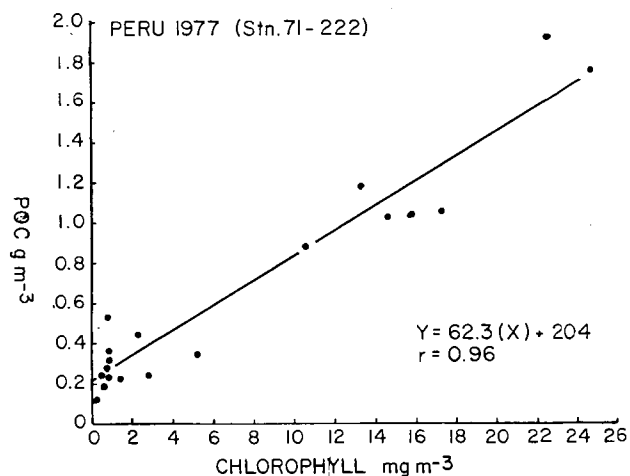


Fig. 6. Vertical nutrient profiles, northern coast of Peru.

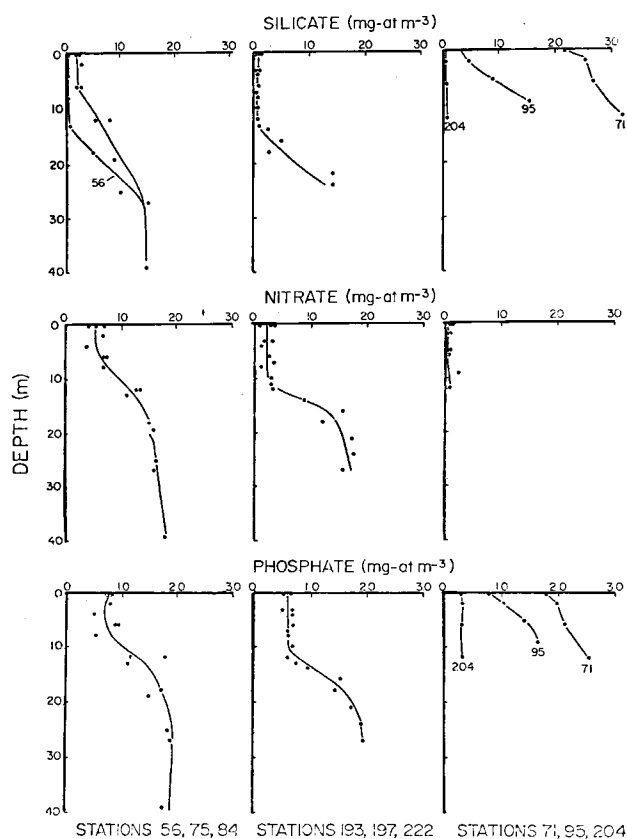


Table 3. Euphotic zone nitrogen concentrations (mg-at m^{-2}), productivities ($\text{mg-at m}^{-2}\text{d}^{-1}$) and turnover times (days), Peru 1977.

Stn.	Lat.	NO_3	ρ_{NO_3}	t_{NO_3}	NH_3	ρ_{NH_3}	t_{NH_3}	(F)
23	5°04'N	214.5	2.26	94.9	44.0	10.20	4.3	0.18
37	0°42'N	96.7	1.66	58.3	14.2	5.01	2.8	0.25
48	3°07'S	171.2	3.93	43.6	32.8	7.78	4.2	0.34
56	6°47'S	283.6	40.70	7.0	45.8	16.99	2.7	0.71
71	8°40'S	4.1	2.59	1.6	52.9	23.49	2.3	0.10
75	8°54'S	526.9	28.38	18.6	9.2	3.57	2.6	0.89
84	9°12'S	99.1	32.59	3.0	4.1	2.77	1.5	0.92
95	9°23'S	9.6	6.40	1.5	2.9	2.12	1.4	0.75
193	9°20'S	205.4	10.94	18.8	26.2	4.56	5.7	0.71
197	9°20'S	141.4	10.35	13.7	13.3	3.62	3.7	0.74
204	8°50'S	2.7	2.35	1.1	2.8	2.58	1.0	0.47
222	9°22'S	<u>178.7</u>	<u>16.35</u>	<u>10.9</u>	<u>42.8</u>	<u>8.23</u>	<u>5.2</u>	<u>0.67</u>
$\bar{x}(71-222)$		146.0	13.74	10.6	19.3	6.38	3.03	0.66

$$(F) = \frac{\rho_{\text{NO}_3}}{\rho_{\text{NO}_3} + \rho_{\text{NH}_3}}$$

Fig. 7. Relationship between nitrate and phosphate concentrations. Open circles are STNS 71 and 95.

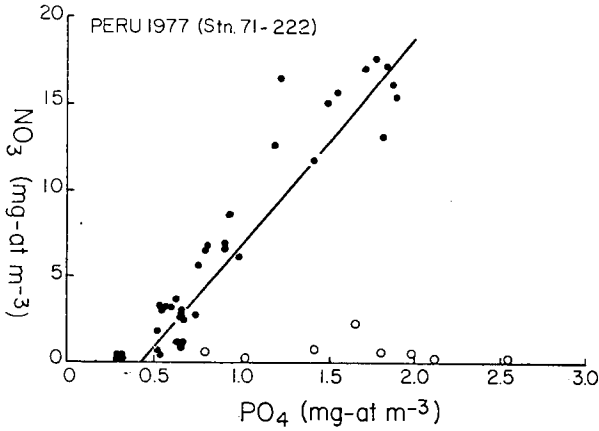


Fig. 8. Relationship between nitrate and silicate concentrations. Open circles are STNS 71 and 95.

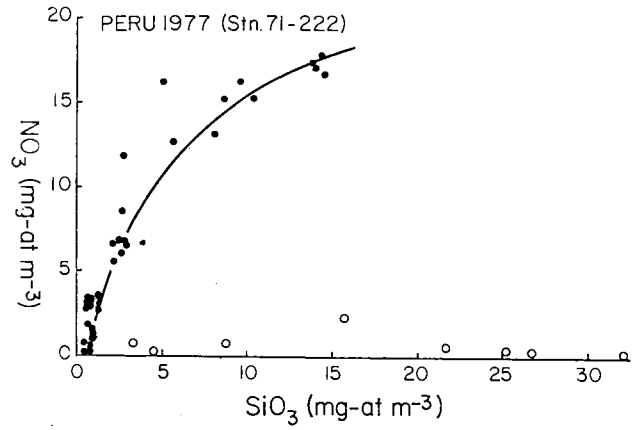


Fig. 9. Ammonia concentrations along onshore-offshore section (ref. fig. 2), northern Peru coast.

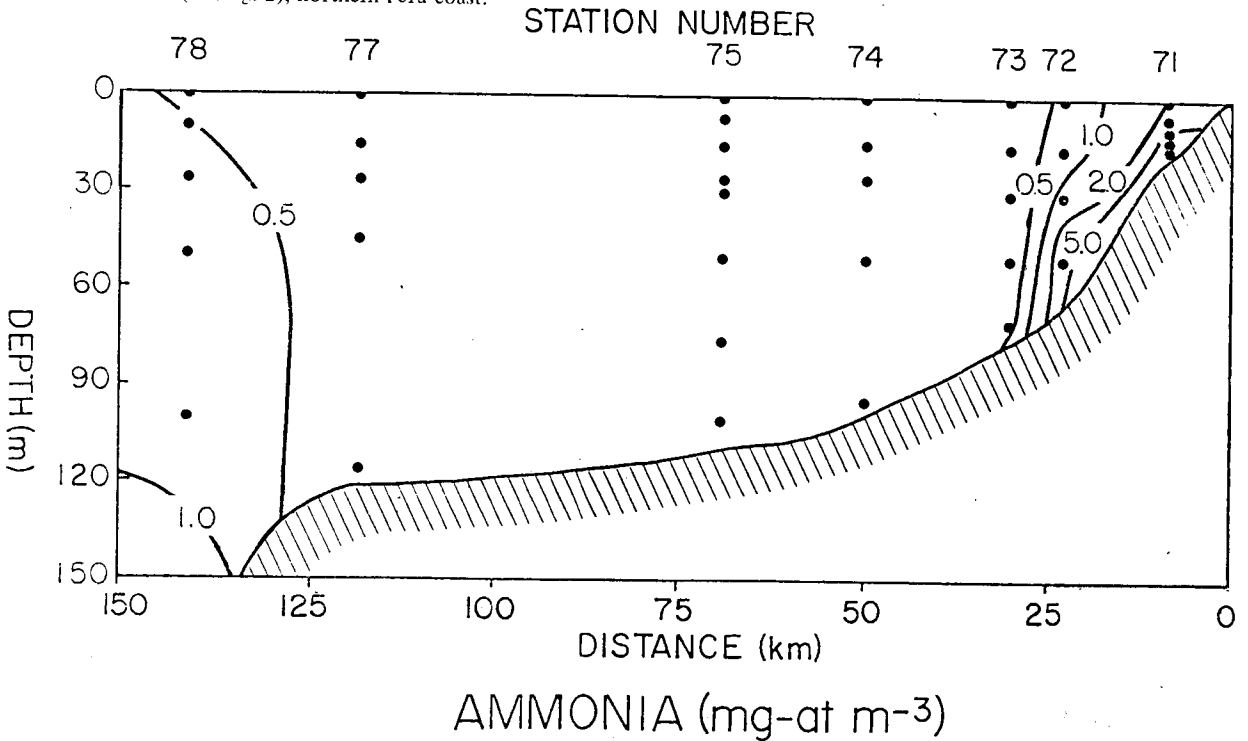


Fig. 10. Frequency distributions of C:N assimilation and particulate compositional ratios.

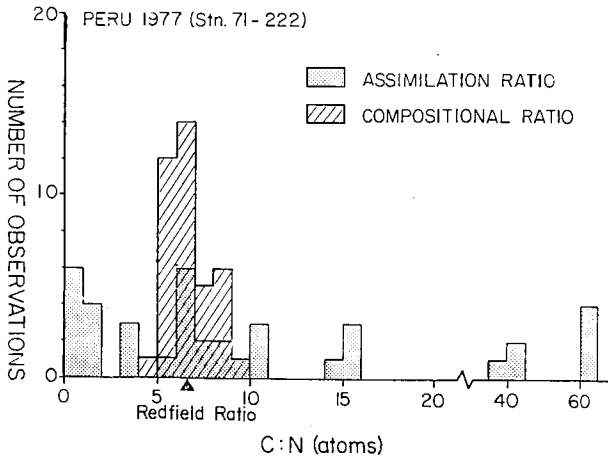
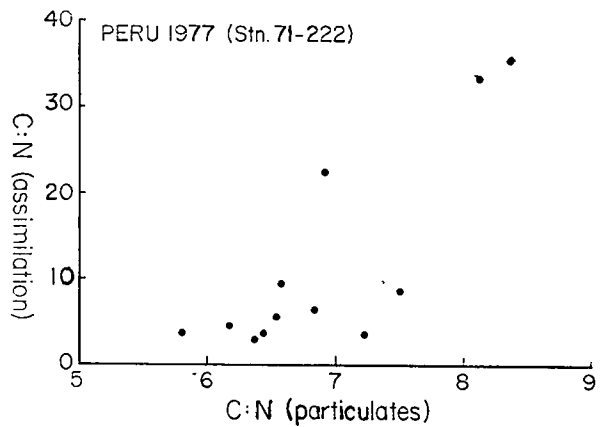


Fig. 11. Relationship between C:N assimilation and C:N composition of the particulate matter.



higher than the Redfield ratio (C:P = 106:1) at the productive inshore stations and decreased offshore. N:P assimilation ratios appeared relatively independent of N:P nutrient ratios (Fig. 13).

Stations could be grouped according to their C:N:P assimilation ratios (Table 4). Based on C:N, C:P, and N:P assimilation ratios, the produc-

Fig. 12. Relationship between C:P assimilation ratio and phytoplankton biomass (Chl).

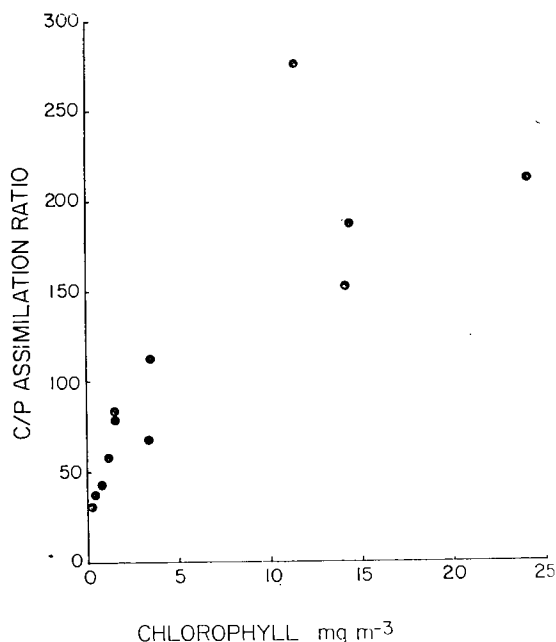
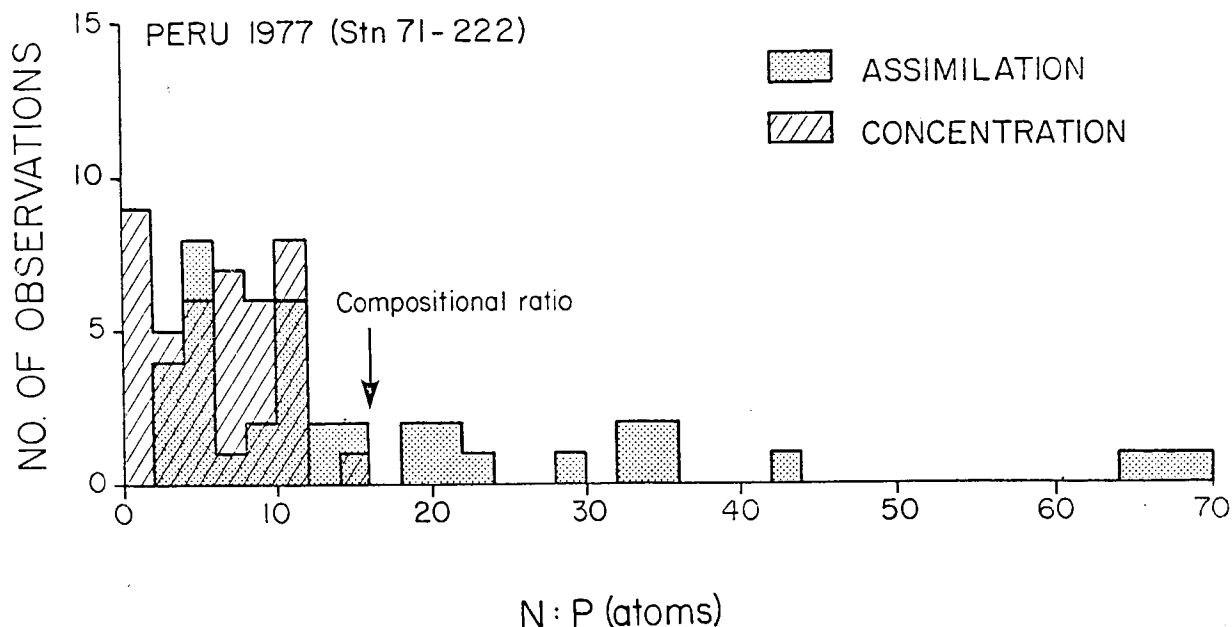


Fig. 13. Frequency distributions of N:P assimilation and nutrient concentrations.

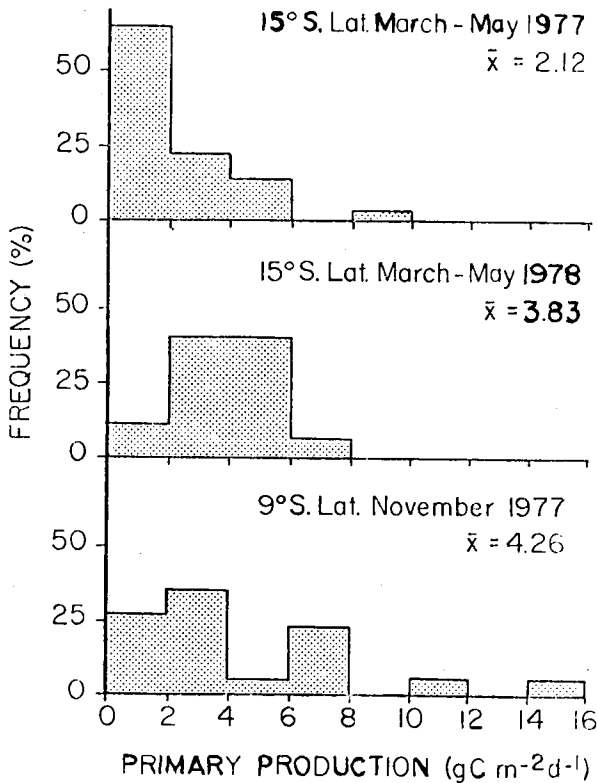


tive inshore stations (STNS 71,95) and the *M. rubrum* (red tide) station (STN 204) exhibited nutrient assimilation ratios suggesting N-limitation (i.e., C:N>6.5, N:P<16). Based on N:P assimilation ratios, STNS 56, 75, 84, and 193 would be assessed as phosphorus limited.

Silicate tracer studies were not done on this cruise but based on NO₃SiO₃ concentration relationships and a lack of correlation between either C or N productivity rates and SiO₃ concentrations (ref. Dugdale, 1972), nitrogen appeared the more important nutrient in controlling primary production during the ICANE study.

5. Comparison with other studies.— Most of the earlier and more recent productivity measurements off the coast of Peru have been concentrated near 15°S Lat. (e.g., Guillen *et al.*, 1977 and; references included; Sorokin and Kogelshatz, 1979, etc.). Barber (unpubl.) has recently compiled productivity data from 15°S Lat. for the period 1966 to 1978. Average values were 6.26 (1966), 5.16 (1969), 1.69 (1977) and 3.83 (1978) g C m⁻²d⁻¹ from March to May. Guillen and Rondan (1968) and Guillen *et al.* (1969, 1977) found approximately 1 g C Fixed m⁻²d⁻¹ further north (7–9°S Lat.) in the area of the present study. These averages were lower than ours (\bar{x} = 4.26 g C m⁻²d⁻¹) but represented a larger data base and much larger sampling area, including offshore (100–200 mi.) waters. Our values are similar to Sorokin's (1978) inshore stations (3–9 g C m⁻² d⁻¹). A comparison of 1978 data from 15°S and 8°S Lat. (Fig. 14) revealed similar mean values yet greater variability in the northern area. We observed values on some occasions in excess of 12 g C m⁻²d⁻¹ which have not previously been recorded at either location except during "red tide" conditions.

Fig. 14. Frequency distributions of primary production at 9° and 15°S Lat. off the coast of Peru in 1977 and 1978.



ACKNOWLEDGEMENT

The authors would like to thank K. Sellner

Table 4. Groupings of stations based on C:N:P assimilation ratios (depth integrated), Peru 1977. Stations to the left of each column exhibited ratios higher than the "Redfield ratio", stations to the right were lower.

C:P 106		C:N 6.6		N:P 16	
>	<	>	<	>	<
71	23	23	48	56	23
84	37	37	56	75	37
95	48	71	75	84	48
204	56	95	84	193	71
	75	204	193		95
	193		197		197
	197		222		204
	222				222

for access to his unpublished productivity data (STNS 251-336) used in Fig. 3 and 4 of this manuscript.

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