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INTRODUCTION

Quantitative benthic samples were taken off Peru in and adjacent to the Pisco upwelling in an attempt to assess the effects of extremes in productivity and dissolved oxygen on the distribution of biomass (organic carbon). The macrofauna was combusted to organic carbon (less the carbonate fraction) to allow direct comparisons with the production of organic carbon at the surface and its distribution in the water column and sediments. Similar techniques were employed in the Gulf of Mexico previously (ROWE and MENZEL, 1970), and it is hoped comparisons of the two sets of data contrasting regions of low and high productivity will give some insights into the nature of the movement of organic energy from its source through the water column to the bottom.

METHODS

Conventional benthic sampling techniques were used which have all been described in detail elsewhere. In shallow water (up through 1000 m) 0.1 and 0.2 m² van Veen grabs were used, whereas at greater depths along the slope of the Milne-Edwards deep, samples were taken with a large anchor dredge. The samples were sieved through 0.42 mm screen and preserved in 10 % buffered formalin. After being sorted to larger taxa in the laboratory, the fauna was weighed wet and dry and com-

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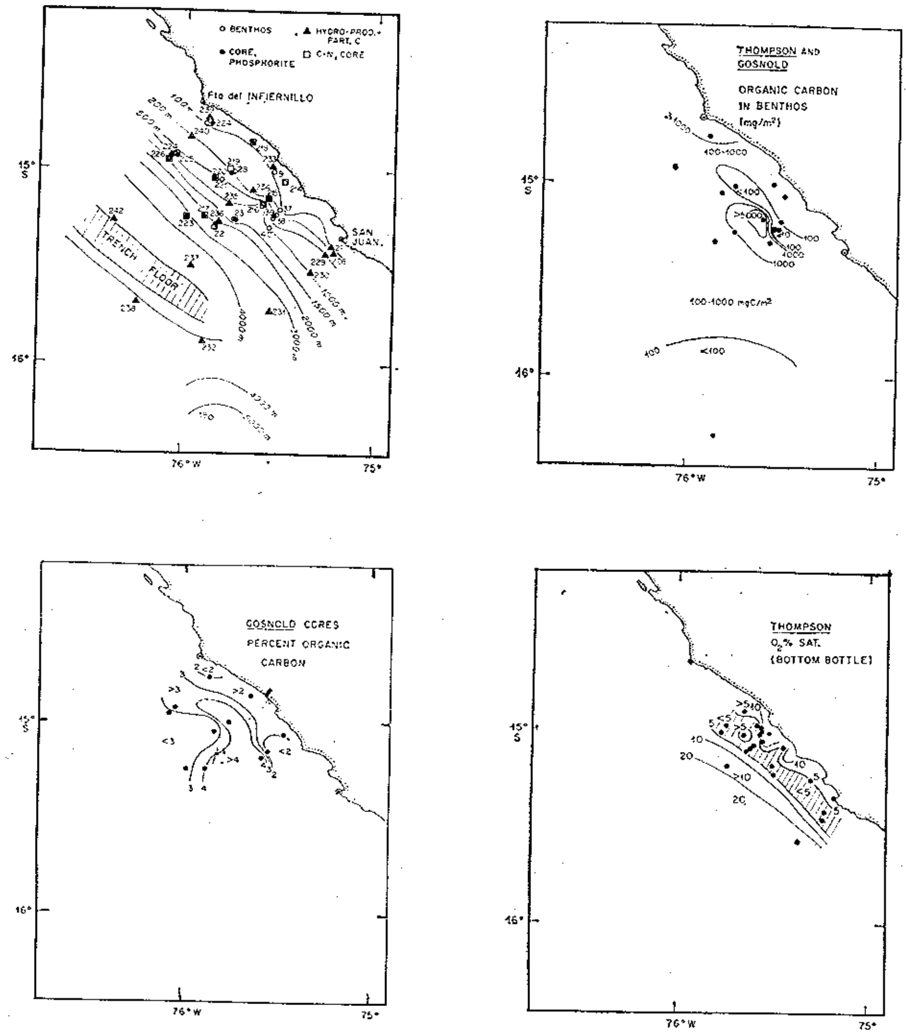

FIG. 1. — *a*) Station locations, benthic data. *b*) Organic carbon in the macrofauna (> .42 mm). *c*) Sediment core data. *d*) Percent saturation of oxygen in water from deepest bottles.

busted (less the carbonate fraction) in a Perkin-Elmer No. 240 Elemental Analyzer to determine organic carbon content. Hydrographic and sediment data were collected with routine techniques which have been mentioned by the other investigators at this conference.

RESULTS

The data taken at the locations plotted (fig. 1*a*) are listed in table I. Benthic biomass estimates dropped from *ca.* 2000 milligrams per square meter on the shelf (85 m) to a minimum of 8 mg C/m² at just over 300 m. From there it rose to a maximum of about 5000 mg C/m² near 1000 m and then diminished in a semi-logarithmic fashion to 41 mg C/m² as depth increased to 5700 m. Data on the bottom water oxygen, topography, sediments and surface productivity were gleened from the reports resulting from ANTON BRUUN, GOSNOLD, and T. G. THOMPSON cruises. Some of these have been contoured in an attempt to infer what controls the erratic, patchy distribution of biomass (fig. 1*c*, *d*). In general, no patterns of reliable consequence emerged because most of these environmental data were themselves so patchy in time and space, and in few cases were the biological and physical data collected at the same locations. Only oxygen concentration, with its minimum impinging on the slope at 100-500 m, appears a likely candidate as a limiting factor.

Several statistical analyses were attempted to assess how and what parameters control biomass (organic carbon) in the benthos. Least squares linear regressions of biomass on depth did not have a slope significantly different from zero. A graph comparing the different environmental variables measured with depth (fig. 2) suggests low concentrations of dissolved oxygen caused a condition of stress which was manifested in low biomass, as has been suggested by others working off Western South America (GALLARDO, 1963 ; FRANKENBERG and MEN-

TABLE I

Biomas (mg C/m²) in macrobenthos (> .42 mm)

	STATION	DEPTH	Nos./m²	mg C/m²
GOSNOLD	214	85	2723	354
	216	875	1519	5385
	221	500	5595	484
	224	85	5740	1952
	225	650	2265	303
T.G.T.	9	73	599	635
	19	5700	122	41
	22	2400	397	647
	23	1458	1596	1052
	28	197	4480	58
	37	144	7680	110
	38	219	7000	69
	39	319	2080	8
	40	1000	488	4360

ZIES, 1968). Lowest estimates of biomass, *ca.* 8 mg C/m², were at our 329 m station, and lowest bottom water oxygen values were between 200 and 300 m (< 0.1 ml/l or < 5 % saturation). At greater depths oxygen concentration increased as did biomass. Maximum estimates were at 800 and 1000 m where oxygen values were greater than 1.0 ml/l

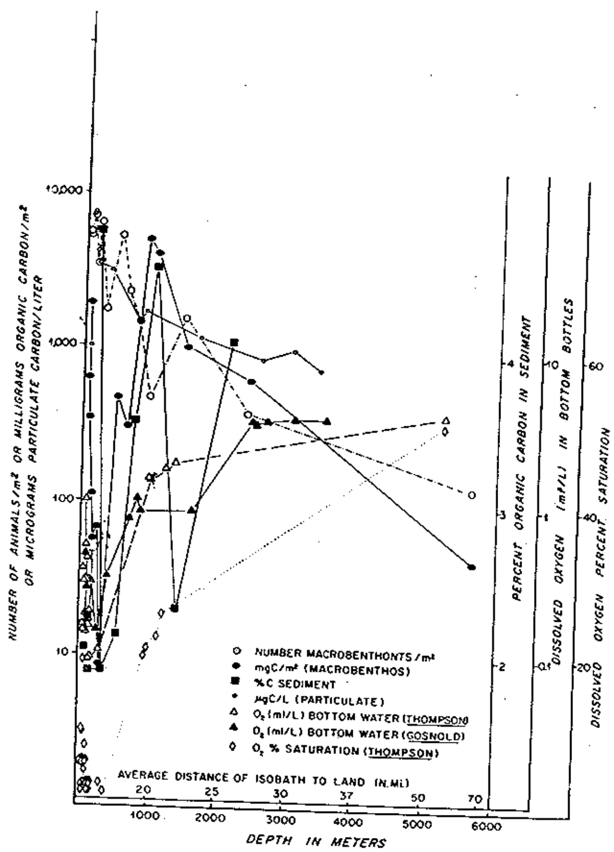

FIG. 2. — A comparison of environmental variables and biomass (organic carbon) estimates with depth and distance from land.

and approached 20 % saturation. At greater depths oxygen continued to increase gradually, whereas biomass dropped. It would not be valid to say that these precise oxygen values were what controlled life because in no case were these taken at the sediment water interface.

The relationships between these data should at first glance be accessible with a multiple regression analysis comparing biomass with both oxigen and depth. Unfortunately, depth is the only variable that can be dealt with as independent, and the oxygen and biomass, although validly regressed on depth, were not taken at the same stations, and therefore statistical comparison of the two is not justified. The correlation on the graph, however, suggests the low biomass in shallow water

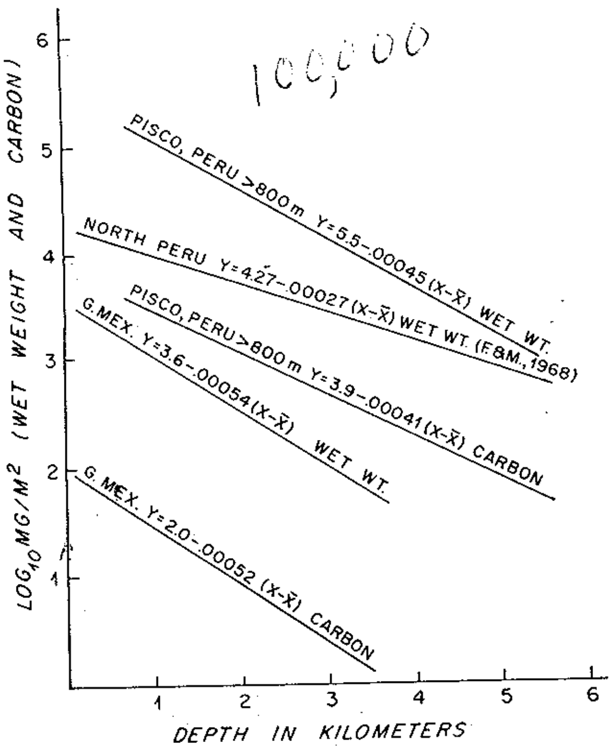

FIG. 3. — Least squares regressions of the logarithm (base 10) of biomass estimates on depth off Peru and in the Gulf of Mexico. The «North Peru» line is a regression of data presented by Frankenberg and Menzies, 1968. The PISCO carbon and weight lines included data only from 800 m and greater. For all five lines $P < .01$ slopes equal zero.

can be assumed to be a manifestation of the stress induced by low oxygen.

Surprisingly, however, this is evidently not the case with numbers of individuals. Least squares linear regression of the logarithm (base 10) of these data on depth indicated animal numbers diminished according to the following relationship : $\text{Log}_{10}X = 3.6 - .00029\ (X\text{-}\bar{X})$ ($p < .001$ $b = 0$). This anomaly of dense populations with low biomass suggests more energy is required for survival in this zone or that turnover rates in the populations (predominately nematodes) are much higher than elsewhere.

Assuming stress on the fauna is caused by low oxygen concentrations, one can estimate what other conditions in the environment also appear related to faunal biomass by eliminating from the regression those samples taken in the zone under stress. Doing this, we found biomass decreased with depth in the following manner :

$$\text{Log}_{10}Y = 3.91 - .00041 (X\text{-}\bar{X}) \ (p = < .01 \ b = 0)$$

This allows an estimation of biomass with depth which could be compared to results in the Gulf of Mexico, a basin without such a pronounced, stressful oxygen minimum.

The rates of disappearance in biomass with depth were not different in the Gulf of Mexico and off Pisco, Peru, based on the data gathered so far (fig. 3). A decrease of approximately one order of magnitude of organic carbon in macrobenthos was found with every 2000 m increase with depth. For the Gulf, it was suggested this five-fold decrease every kilometer down must result from energy loss in the water column (ROWE and MENZEL, 1970). The longer the water column, the less food reaches the benthos, which suggests there is loss through zooplankton food chains much like that suggested by VINOGRADOV (1962), who demonstrated that a logarithmic relationship exists between zooplankton and depth (1969).

DISCUSSION

Although the rates (slopes) in the Gulf and Peru appear the same, absolute quantities differ markedly between the two areas. The relatively non-productive southern Gulf of Mexico has two orders of magnitude less biomass than the productive Peru upwelling at equivalent depths, where the benthos did not appear limited by low oxygen concentrations.

These two sets of data, along with the primary productivity data available from the literature and presented at this conference, can be used to make further inferences about relationships of organic production and ecosystem energy flow.

A safe approximation for euphotic primary organic production in the offshore Gulf water would probably be 0.2-0.5 g C/m^2/day (CORWIN, 1969), while off Peru it would range from about 2-5 g C/m^2/day (RYTHER, 1969). In any case, average productivity can be estimated to be 10-50 times greater off Peru than in the Gulf, whereas biomass regressions on depth (again eliminating oxygen minimum depths) suggest there is 100 times more biomass in deep water off Peru than in the Gulf at equivalent depths. This apparent disparity has several implications concerning energy flow, each of which deserves some consideration.

If it is assumed energy production should be reflected directly in energy utilization, and that turnover or metabolic rates are the same in both areas and at all depths, then there should be about ten times as much biomass off Peru than in the Gulf, rather than 100. One of the several explanations of this disparity is that there is little removal of organic material from the upper 1000 m or so off Peru as compared to the Gulf, which would tend to shift the regression line for Peru to the right. Initially this appears to be the most acceptable explanation, because it is reasonable that little utilization of energy would occur in the extreme oxygen minimum by chemical oxidation. Likewise, one might expect a decrease in biological activity in the zooplankton in terms of respiration and feeding in the oxygen minimum (VINOGRADOV and VORONINA, 1961). These would both contribute to allowing much more food reach the bottom off Peru than expected, as compared to equivalent depths in the Gulf.

Another possibility is that organic rich sediments have a greater tendency to move down the steep topographic gradient off Peru than in the Gulf of Mexico. Although no correlation could be found between biomass and percent organic carbon in the sediments in the Gulf (ROWE and MENZEL, *op. cit.*), as well as with the data presented here, the average percent organic carbon for 11 samples taken from 85 m to 3350 m off Peru was *ca.* 5 times (2.88 %, 1.88-4.75) that at 13 stations taken at 190-3700 m (0.58 %, 0.19-1.21) in the Gulf. This suggests that although correlations within individual basins have not been found, sediment organic material deserves considerable consideration as a possible deep-sea food supply, whatever its origin (SOKOLOVA, 1968).

Another explanation may be related to the efficiency with which organic energy passes through the ecosystem. If the individuals in the water column as well as the benthos can feed more efficiently off Peru as a result of the greater initial production, if food chains in the Gulf have more links than off Peru, or if organic material sinks more rapidly off Peru, then more biomass would be found off Peru than expected from our hypothetical relationship.

CONCLUSIONS

Attempts to estimate benthic biomass relative to physical parameters in the Pisco, Peru upwelling have met with only a modicum of success due to the extremes encountered in productivity, dissolved oxygen, and there is 100 times more biomass in deep water off Peru than in the Gulf at equivalent depths. This apparent disparity has several implications concerning energy flow, each of which deserves some consideration.

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Attempts to estimate benthic biomass relative to physical parameters in the Pisco, Peru upwelling have met with only a modicum of success due to the extremes encountered in productivity, dissolved oxygen, and sediment characteristics. It appeared that conditions of stress were induced by dissolved oxygen concentrations of less than 20 % saturation. The semi-logarithmic, inverse relationship generally encountered between biomass and depth was found only when data from depths greater than the oxygen minimum were used. The standing crops of biomass in the deep water off Peru were 100 times those in the Gulf of Mexico at equivalent depths, rather than 10-50 times greater as expected when the primary productivities of the two areas are compared. Among the suggestions to explain this disparity, the most acceptable is that more food reaches bottom off Peru than expected due to a decrease in biological and chemical loss of potential food as it sinks or is carried through the oxygen minimum.

SUMMARY

Quantitative benthic faunal samples in the Pisco, Peru upwelling were combusted to organic carbon in an attempt to relate this measure of biomass to carbon production, carbon distribution throughout the ecosystem, and to parameters in the environment. Biomass of the benthos was inversely related to depth, but also related directly to surface primary productivity. These relationships were overridden by stress conditions induced by low oxygen concentration. A comparison of surface production and benthic biomass in the Gulf of Mexico and off Peru suggested that biomass diminished with depth at equivalent rates in the two basins, but that there was more biomass in Peru than expected on the basis of primary production.

RESUMEN

Biomasa bentónica en el afloramiento de Pisco, Perú. — Muestras cuantitativas del bentos recolectado bajo el afloramiento de Pisco, en el Perú, se analizaron en términos de carbono orgánico, por combustión, en un intento de establecer relaciones entre esta medida de la biomasa y la producción y distribución de carbono a través de todo el ecosistema, así como con parámetros ambientales. La biomasa del bentos está inversamente relacionada con la profundidad, y guarda relación directa con la productividad. Estas relaciones se ven dominadas por los efectos de la baja concentración de oxígeno. El estudio comparativo de la producción en superficie y de la biomasa bentónica, en el Golfo de Méjico y en las costas de Perú, indica que la biomasa decrece en la misma tasa en las dos cuencas, pero que en el Perú la biomasa es superior a la que se podría esperar dada la producción primaria.

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