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# Anomalous nutrient-chlorophyll interrelationships in the offshore eastern tropical Pacific Ocean

by William H. Thomas<sup>1</sup>

## ABSTRACT

In the nutrient-rich offshore areas of the eastern tropical Pacific Ocean, chlorophyll levels were 4-10 times lower than might be expected if all the inorganic nitrogen had been assimilated. Three hypotheses are examined to explain this anomaly: 1) nitrate may be upwelled faster than it is assimilated; 2) the algae may be grazed to lower levels by herbivores; and 3) minor nutrients other than nitrate, phosphate, or silicic acid may be limiting. The grazing hypothesis seems most likely in the Costa Rica Dome; all three hypotheses may operate in the equatorial upwelling area; and minor nutrients may be limiting in the southerly nutrient-rich water.

## 1. Introduction

The EASTROPAC Expedition of 1967-68 definitively showed areas in the eastern tropical Pacific Ocean where near-surface nutrient concentrations—nitrate-N, phosphate-P, and silicic acid—are low as contrasted with other areas where upwelling or advection increase the levels (Thomas, 1970a, 1971, 1972a, 1974). My purpose is to point out that chlorophyll levels in offshore nutrient-rich areas were not as high as they might be if all nutrients were assimilated. Hypotheses to explain this anomaly are based mainly on postulated nitrate assimilation, since nitrogen is the principal limiting nutrient over much of the region (Thomas, 1969).

Figure 1 shows the distribution of near-surface nitrate in February-March 1967 in three offshore nutrient-rich areas: the Costa Rica Dome, an area of offshore upwelling centered about 90W longitude and 10N latitude; the equatorial upwelling area, extending along the equator west of the Galápagos Islands; and the southerly nutrient-rich water extending from longitudes 98°-126°W at 8°-12°S latitude. These two latter areas are not greatly distinguished from each other in Figure 1; in the equatorial area a source of nutrient-rich water underlies the surface layers, while in the southerly nutrient-rich area, nutrient-poor water underlies the rich near-surface water (Thomas, 1972b). Data from other EASTROPAC cruises in 1967-68 show

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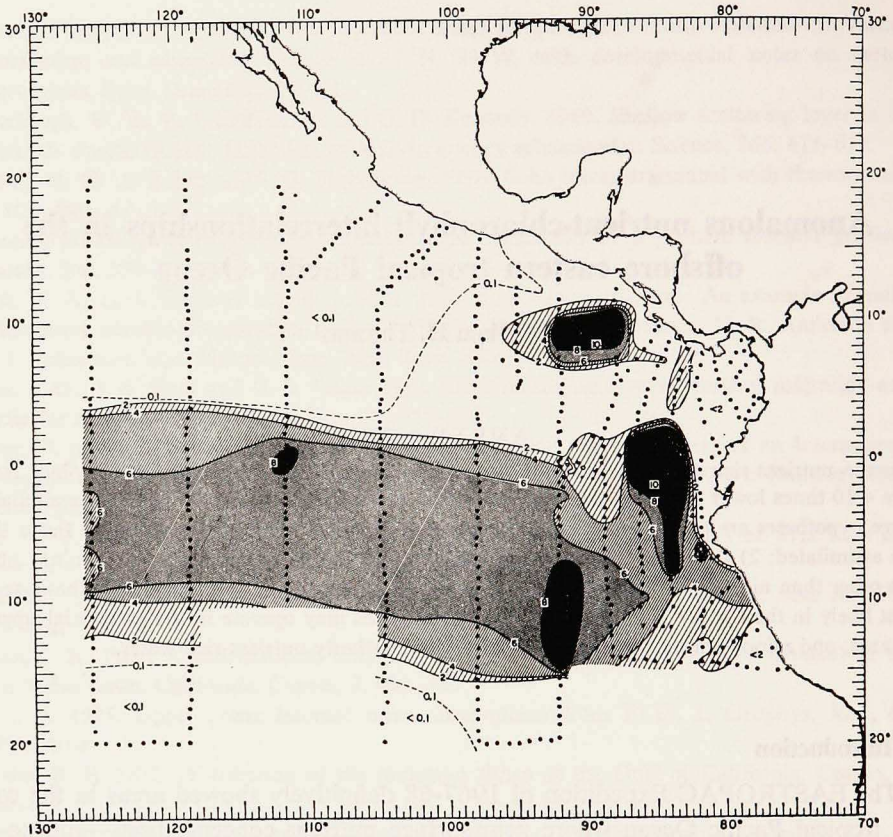


Figure 1. Nitrate-nitrogen ( $\mu\text{g-at/l}$ ) at 10 meters, February-March, 1967 (from Thomas, 1971).

that nutrient-rich water persisted in these regions at other seasons; this was not the case for the pronounced dome shown in Figure 1 east of the Galápagos. In the Costa Rica Dome and along the equator, near-surface nitrate levels ranged from 6-10  $\mu\text{g-at NO}_3\text{-N/l}$ ,  $\text{PO}_4\text{-P}$  from 0.6-1.0  $\mu\text{g-at/l}$  and  $\text{SiO}_2\text{-Si}$  from 6-8  $\mu\text{g-at/l}$ . In the southerly nutrient-rich water, levels were lower, with  $\text{NO}_3\text{-N}$ ,  $\text{PO}_4\text{-P}$  and  $\text{SiO}_2\text{-Si}$  ranging from 2-6, 0.4-0.6, and 2-4  $\mu\text{g-at/l}$ , respectively.

During March-April 1968 (EASTROPAC Cruise 76) natural phytoplankton assemblages from nutrient-poor water incubated aboard ship with different inorganic nitrogen concentrations yielded about 0.2  $\mu\text{g}$  of chlorophyll per  $\mu\text{g-at N}$  added (Thomas, 1970b). A similar yield figure was found in unpublished experiments with a dinoflagellate, *Gymnodinium simplex*, isolated from the Costa Rica Dome.

If all the near-surface nitrate in these three areas were assimilated by phytoplankton, we might expect 1.2-2  $\mu\text{g}$  chlorophyll/l in the surface waters of the Dome, 1.2-1.6 at the equator, and 0.4-1.2 in the southerly rich water. These are conserva-

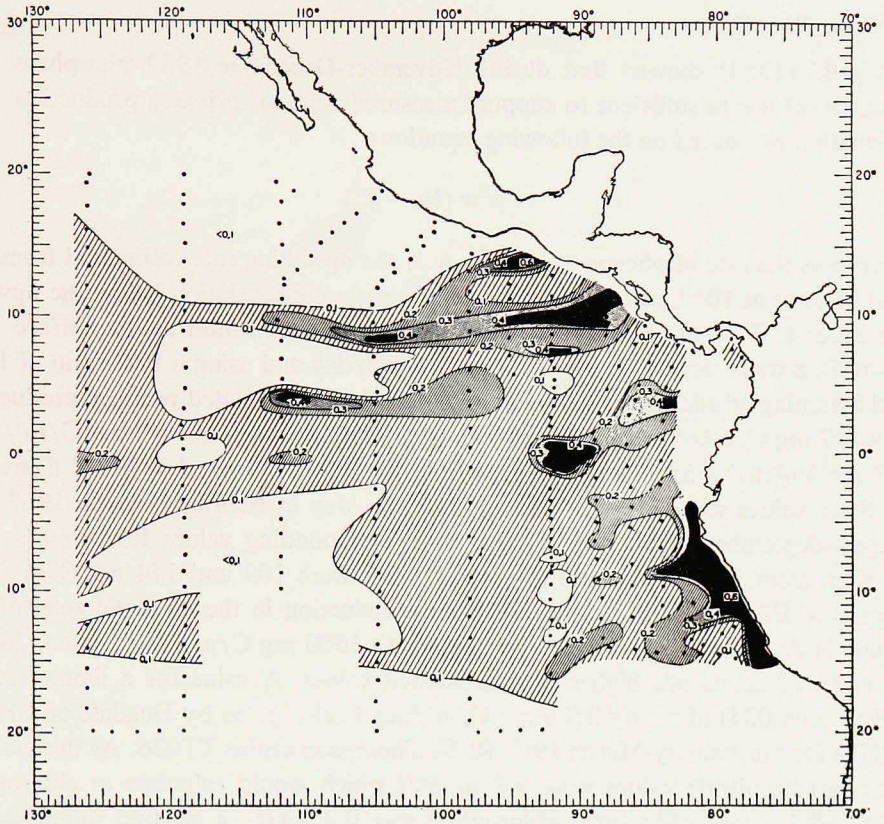


Figure 2. Chlorophyll-a ( $\mu\text{g}/\text{l}$ ) at the sea surface, February-March, 1967 (from Owen, 1971).

tive estimates, since other workers have found yields of  $1.0 \mu\text{g}$  of chlorophyll per  $\mu\text{g-at N}$  added (Eppley, personal communication). Measured surface chlorophyll levels during the February-March 1967 cruise are shown in Figure 2 (Owen, 1971). These levels were  $0.2\text{-}0.4 \mu\text{g}$  chlorophyll/ $\text{l}$  in Dome waters;  $0.1\text{-}0.2$  at the equator, and  $\leq 0.1$  in the southerly rich water, with similar levels found in these areas at other seasons (Owen, 1970, 1972, 1974). Thus, measured chlorophyll concentrations were some 4-10 times lower than might be expected from nitrate concentrations. These considerations exclude potential assimilation of ammonium which ranged up to  $1.0 \mu\text{g-at}/\text{l}$  in these waters; of nitrite, which can reach  $0.2 \mu\text{g-at}/\text{l}$ ; or of available organic nitrogen sources such as urea, which was not measured.

Three hypotheses can be examined to explain these anomalies. First, in upwelling regions, nitrate may be upwelled faster than it is assimilated. Secondly, the algae may be grazed by herbivores so that chlorophyll levels are reduced. Third, other nutrients such as trace metals or vitamins may limit algal growth.

## 2. Costa Rica Dome

Wyrтки (1964) showed that during November-December 1959 phosphate was upwelled at a rate sufficient to support measured rates of primary production. His calculation was based on the following equation:

$$x = w (P_D - P_0)$$

where  $x$  is the rate of phosphate supply,  $w$  is the upwelling rate (estimated from the heat balance at  $10^{-4}$  cm/sec),  $P_D$  is the phosphate concentration below the upwelling water ( $2.3 \mu\text{g-at/l}$ ) and  $P_0$  is the phosphate concentration at the surface ( $0.5 \mu\text{g-at/l}$ ).  $x$  was calculated to be  $155 \mu\text{g-at P/m}^2/\text{day}$  and using a P/C ratio of 1:41 and assuming all the upwelled P was assimilated, the calculated primary production was  $197 \text{ mg C/m}^2/\text{day}$ . Measured primary production was  $160\text{--}440 \text{ mg C/m}^2/\text{day}$ .

I recalculated  $x$  for nitrate using the EASTROPAC data and Wyrтки's figure for  $w$ ; the  $x$  values were 130 and  $210 \mu\text{g-at N/m}^2/\text{day}$  in February-March 1967 and August-September 1967, respectively. The corresponding values for primary production, assuming a C/N ratio (by atoms) of 7, were 109 and  $174 \text{ mg C/m}^2/\text{day}$ . Measured EASTROPAC levels of primary production in the euphotic zone of the Dome in August-September 1967 ranged up to  $1500 \text{ mg C/m}^2/\text{day}$  (Owen, 1970), an order of magnitude higher than calculated values. A value for a Dome station (*Thompson* 034) of nearly  $2500 \text{ mg C/m}^2/\text{day}$  is also given by Dugdale and Healy (1971) for the January-March 1968 R. V. *Thompson* cruise TT026. At this station, near-surface nitrate values were  $9.2 \mu\text{g-at/l}$  which would calculate to chlorophyll levels of  $1.8 \mu\text{g/l}$ . Measured chlorophyll was  $0.8 \mu\text{g/l}$ —a twofold difference. A more extreme anomaly is calculated for *Thompson* station 36 where nitrate levels reached  $16 \mu\text{g-at/l}$ , yet the measured chlorophyll values were only  $0.2 \mu\text{g/l}$ . The calculated value of chlorophyll would be  $3.2 \mu\text{g/l}$ . At this time the  $26^\circ\text{C}$  isotherm was outcropping at the Dome (Tsuchiya, 1972), and Wyrтки (1964) noted that  $w$  would be greater than  $10^{-4}$  cm/sec under such conditions. This may explain the discrepancy between measured and calculated rates of production. These comparisons do not indicate an upwelling rate at the Dome that was faster than assimilation. At the Dome, zooplankton volumes were elevated (Laurs, 1970, 1971, 1972, 1974) during January-February 1967 (see Fig. 3) and also during August-September 1967. A comparison of phaeopigment/chlorophyll ratios, which might be a measure of past grazing, at the Dome and in northerly nutrient-poor water showed that the ratios were not elevated at the Dome. This was the case for the three times the Dome was visited during EASTROPAC: February-March 1967, August-September 1967, and February-March 1968. However, maps of near-surface phaeopigment concentrations showed that this parameter (not the ratio) was elevated at the Dome during the first two cruises, but not during the last cruise (Owen, 1971, 1972, 1974). Elevated zooplankton volumes and phaeopigment concentrations indicate that grazing

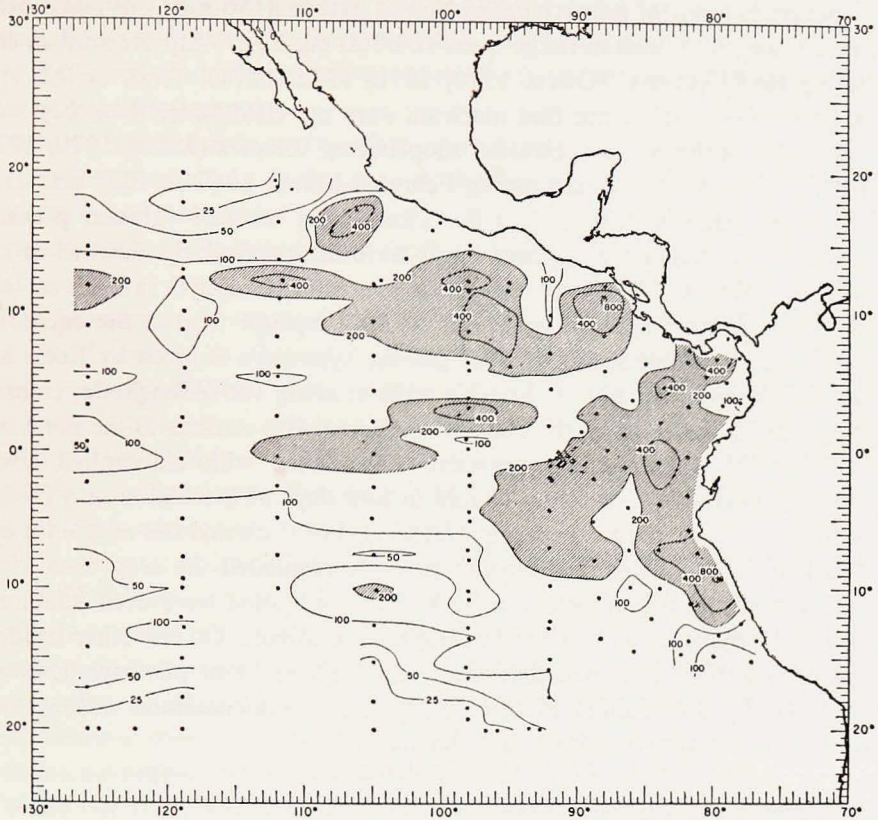


Figure 3. Distribution of standing stock ( $\text{ml}/1000 \text{ m}^3$ ) of zooplankton taken in 50-cm net hauls at night, February-March, 1967 (from Laurs, 1971).

might be a valid explanation for the low chlorophyll levels in this area, even though the phaeopigment/chlorophyll ratios were not elevated. The third hypothesis, that other nutrients were limiting, may or may not explain the Dome chlorophyll anomaly. Additions of amino acids or vitamin  $B_{12}$  in a 1956 experiment (Jones and Thomas, 1958) showed a tendency to enhance photosynthetic  $^{14}\text{CO}_2$  uptake, but the effects were not great.

### 3. Equatorial upwelling area

In this area,  $w$  has been variously estimated from data of other cruises to be  $0.5 - 8 \times 10^{-3} \text{ cm/sec}$  (Knauss, 1966; Taft and Jones, 1973). During EASTROPAC,  $N_D$ , the nitrate level below the thermocline, was about  $20 \mu\text{g-at NO}_3\text{-N/l}$ , and  $N_0$  was about  $6 \mu\text{g-at NO}_3\text{-N/l}$ . One can solve for  $x$ , the rate of supply of nitrate, from Wyrтки's (1964) equation.  $x$  ranges from 6000 to 97000  $\mu\text{g-at N/m}^2\text{/day}$ . These

values convert to levels of primary production of 510 to 8150 mg C/m<sup>2</sup>/day. Measured values for <sup>14</sup>CO<sub>2</sub> uptake range from 100-700 mg C/m<sup>2</sup>/day for various seasons during EASTROPAC (Owen, 1970, 1971, 1972, 1974). Thus, in this area there seems to be some chance that nutrients were upwelled faster than they were assimilated. Along the equator, elevated zooplankton volumes (Laurs, 1970, 1971, 1972, 1974) (Fig. 3) were found during February-March 1967 at 105° and 112° longitudes; the volumes decreased to the west. These elevated volumes persisted during 1967. However, phaeopigment levels were not particularly elevated in this area (Owen, 1971, 1972, 1974), and phaeopigment/chlorophyll ratios were statistically higher in nutrient-poor water north of the equator than in the equatorial upwelling zone. Evidence supporting the grazing hypothesis is given by Beers and Stewart (1971), who showed that during a transect along 105W longitude, crops of microzooplankton increased at the equator compared with stations to the north and south, and herbivore crops were positively correlated with chlorophyll levels. Furthermore, chlorophyll increased 10-fold in four days of incubation in a 20-liter sample free of grazers in an experiment (Thomas, 1969) carried out at 0°44'S latitude and 126°02'W longitude. Inorganic nitrogen stimulated the crop even more, while other nutrients did not seem to be limiting and some were even inhibitory, discounting the hypothesis involving limiting trace nutrients. On the other hand, at the equator and 92W, Barber and Ryther (1969) showed that photosynthesis was increased only by the addition of chelating agents or a zooplankton extract. Such organics may make trace metals more available.

#### **4. Southerly nutrient-rich water**

This water at 8-12S latitude is of particular interest. Here nutrient distributions form an inversion (Thomas, 1972b) with a very low concentration at 50-100 meters, compared to near-surface or surface water, and upwelling would not enrich the surface layers. It is also unlikely that nutrient-rich water has advected south from the equatorial upwelling zone, since surface currents in this area typically flow from east to west (Wyrtki, 1966). It is remarkable that water advected thousands of kilometers from the Peru Current has not been depleted of nutrients by phytoplankton assimilation. The grazing hypothesis seems unlikely, since zooplankton volumes were low (see Figure 3). However, chlorophyll increased 10-fold in four days of incubation without added nutrients at 8°41'S latitude and 119°00' longitude (Thomas, 1969). Minor nutrients may very well be limiting, since the addition of EDTA or vitamins to this water resulted in pronounced further increases in chlorophyll, similar to the results of Barber and Ryther (1969).

#### **5. Discussion**

Low-chlorophyll, high-nutrient water is not unique to these offshore regions. Off Peru, "blue" water containing 2 µg chlorophyll/l and 10 µg-at NO<sub>3</sub>-N/l was found

by Strickland *et al.* (1969). These authors suggested that grazing was depleting the water of phytoplankton. On the other hand, in similar water off Peru, Barber *et al.* (1971) showed that photosynthesis could be increased by the addition of trace metals or chelating agents.

Another hypothesis to explain these anomalies is that phytoplankton are mixed out of the euphotic zone so that they are light-limited. This would not apply to the near-surface phytoplankton assemblages discussed herein. Also at the Dome and along the equator the mixed-layer depth was 10 meters during the EASTROPAC cruises, while it reached 60 meters in the southerly nutrient-rich water (Tsuchiya, 1972). Corresponding depths of the euphotic zone were 40-50 meters, 45-85 meters, and 55-65 meters in the three areas, respectively (Owen, unpublished data). Furthermore, calculations of Sverdrup's (1953) critical depth from incident radiation and Secchi depth values always showed that the critical depth exceeded 300 meters (and was even as high as 1100 meters) in all three areas, but always exceeded the depth of the mixed layer. Thus, it is highly unlikely that the algae were ever light-limited due to mixing out of the euphotic zone.

At the equator, there may be bands of high chlorophyll that would be missed by the EASTROPAC sampling stations, so that the idea of anomalous low values would be negated. Examination of continuous analogue chart records of *in vivo* fluorescence in near-surface water taken during the Expedition showed that near the boundary of nutrient-poor and nutrient-rich water there were increases in chlorophyll between stations. These increases were never greater than twofold, and our ideas are not negated, since the anomaly was 4- to 10-fold at least.

Walsh (1976), in a theoretical paper, discusses the relationships between nutrient utilization and grazing in the sea. He divides the sea into three regions: rich coastal areas, equatorial divergences (with which we are concerned herein) and oligotrophic central gyres. Algae in the equatorial zones seem to have the capabilities to grow as well as those in the coastal zones, since assimilation numbers (mg C/mg chlorophyll/hour) are similar. Indeed, at the equator they are not much greater than those in oligotrophic northerly water (Thomas, 1970c). Walsh also points out the apparent paradox of high-nutrient, low-chlorophyll water along the equator, which I have quantified herein, and suggests that this anomaly is due to physical stability within the region which allows continuous algal growth followed by continuous grazing. While grazing may be the most important factor controlling the phytoplankton in these offshore areas, other hypotheses should be examined, and further field work may clarify the importance of various processes in explaining the anomaly of high-nutrient, low-chlorophyll water.

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## REFERENCES

- Barber, R. T. and J. H. Ryther. 1969. Organic chelators: Factors affecting primary production in the Cromwell Current upwelling. *J. Exp. Mar. Biol. Ecol.*, 3, 191-199.
- Barber, R. T., R. C. Dugdale, J. J. MacIsaac, and R. L. Smith. 1971. Variations in phytoplankton growth associated with the source and conditioning of upwelling water. *Inv. Pesq.*, 35, 171-193.
- Beers, J. R. and G. L. Stewart. 1971. Microzooplankters in the plankton communities of the upper waters of the eastern tropical Pacific. *Deep-Sea Res.*, 18, 861-883.
- Dugdale, R. C. and M. L. Healy. 1971. Physical, chemical and productivity data from an investigation of the northeastern tropical Pacific Ocean. R/V *Thomas G. Thompson* Cruise 026 (PONCHO) 3 Jan.-14 Mar. 1968, Univ. of Wash. Tech. Rept. No. 250, 162 pp.
- Jones, G. E. and W. H. Thomas. 1958. The effects of organic and inorganic micronutrients on the assimilation of  $C^{14}$  by planktonic communities and on bacterial multiplication in tropical Pacific sea water, in Physical, chemical and biological oceanographic observations obtained on Expedition SCOPE in the eastern tropical Pacific November-December 1956, Holmes, R. W., ed., Spec. Sci. Rep. U.S. Fish Wildl.—Fish, 279.
- Knauss, J. 1966. Further measurements and observations on the Cromwell Current. *J. Mar. Res.*, 24, 205-240.
- Laurs, R. M. 1970. Contributor to Vol. 4, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1971. Contributor to Vol. 2, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1972. Contributor to Vol. 6, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1974. Contributor to Vol. 8, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- Owen, R. W., Jr. 1970. Contributor to Vol. 4, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1971. Contributor to Vol. 2, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1972. Contributor to Vol. 6, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1974. Contributor to Vol. 8, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- Strickland, J. D. H., R. W. Eppley, and Blanca Rojas de Mendiola. 1969. Poblaciones de fitoplancton, nutrientes, y fotosíntesis en aguas costeras Peruanas. *Bol. Inst. Mar Peru*, 2, 4-45.
- Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. *J. Cons. perm. int. Explor. Mer*, 18, 287-295.
- Taft, B. A. and J. H. Jones. 1973. Measurements of the equatorial undercurrent in the eastern Pacific, in *Progress in Oceanography*, Vol. 6, Warren, B. A., ed., Pergamon Press, Oxford, 193 pp.
- Thomas, W. H. 1969. Phytoplankton nutrient enrichment experiments off Baja California and in the eastern equatorial Pacific Ocean. *J. Fish. Res. Bd. Canada*, 26, 1133-1145.
- 1970a. Contributor to Vol. 4, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1970b. Effect of ammonium and nitrate concentration on chlorophyll increases in natural tropical Pacific phytoplankton populations. *Limnol. Oceanogr.*, 15, 386-394.

- 1970c. On nitrogen deficiency in tropical Pacific oceanic phytoplankton: Photosynthetic parameters in poor and rich water. *Limnol. Oceanogr.*, 15, 380–385.
- 1971. Contributor to Vol. 2, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1972a. Contributor to Vol. 6, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- 1972b. Nutrient inversions in the southeastern tropical Pacific Ocean. *Fish. Bull., U.S.*, 70, 929–932.
- 1974. Contributor to Vol. 8, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- Tsuchiya, M. 1972. Contributor to Vol. 5, EASTROPAC Atlas, C. Love, ed. U.S. Nat. Mar. Fish. Serv. Circ. 330.
- Walsh, J. J. 1976. Herbivory as a factor in patterns of nutrient utilization in the sea. *Limnol. Oceanogr.*, 21, 1–13.
- Wyrki, K. 1964. Upwelling in the Costa Rica Dome. *Fish. Bull., U.S.*, 63, 355–372.
- 1966. Oceanography of the eastern equatorial Pacific Ocean, *in* *Oceanogr. Mar. Biol. Ann. Rev.*, Vol. 4, Barnes, H., ed. Hafner, New York, 505 pp.