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THE SIZE DISTRIBUTION OF PARTICLES IN THE OCEAN[1]

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ABSTRACT

Frequency distributions of particle size between sizes of about 1 and 100 μ are given for both surface and deep water of the Atlantic and Pacific Oceans. The form of the size spectra varies predictably both geographically and with depth. A hypothesis is presented to show that, to a first approximation, roughly equal concentrations of material occur at all particle sizes within the range from 1 μ to about 10^6 μ, i.e. from bacteria to whales.

INTRODUCTION

The gross distribution of total suspended particulate matter in the sea is relatively well documented, but very little is known of the distribution of particle size and of its variation areally and with depth. Some attempts have been made to estimate particle size from optical measurements (e.g. Burt 1958), but the prevailing opinion at present seems to be that optical determinations can do little more than indicate that most of the particles in the sea are large relative to the wavelength of light (Jerlov 1968). Size fractionation by means of screens and filters has been tried (e.g. Mullin 1965; Saijo 1964), but the results of the filter fractionations are questionable (Sheldon and Sutcliffe 1969). Microscopic methods have been used, and these probably give reasonably accurate estimates of particle size, but even when semiautomated they are tedious and time consuming. The particle volume data given by Krey (1967) indicate a mean equivalent spherical diameter of about 5–6 μ for particles in the surface waters of the North Atlantic. At a depth of 500 m the mean size was slightly more than 6 μ. Recent work by Gordon (1970) has shown that particles are numerically most abundant at small sizes (<7 μ), and there is no significant change in size distribution with depth.

The development of electronic methods has greatly simplified the process of counting and sizing marine particles (Sheldon and Parsons 1967*a*). In this paper we present results of electronic determinations of particle size for material in suspension in the Atlantic and Pacific Oceans.

We would like to thank Coulter Electronics, Inc., for the loan of a model T Coulter counter. This helped our work in the Pacific considerably. We would also like to thank Duke University for providing ship time on RV *Eastward* and Dr. C. T. Schafer for allowing us to examine his North Pacific zooplankton samples.

MATERIALS AND METHODS

Surface-water samples were collected from the Atlantic, Pacific, and Southern

[1] Bedford Institute Contribution.

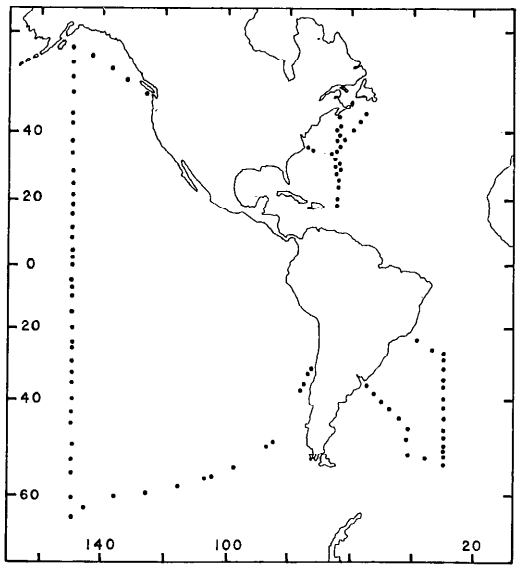

FIG. 1. Location of sample stations.

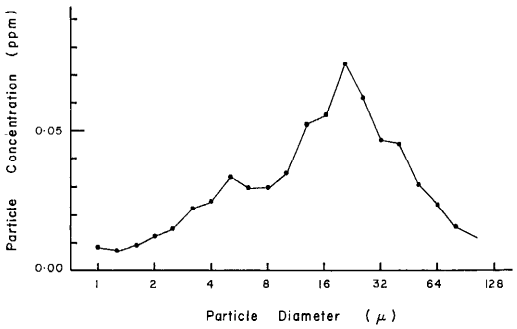

FIG. 2. Size-frequency distribution; to show the notation of the axes and the least number of data points used to define the form of the distribution. Concentration is *by volume*. All the size-frequency distributions in Figs. 3–9 were constructed in this way.

Oceans (Fig. 1). Deep-water samples were taken only from the North Atlantic, the South Pacific, and the Southern Ocean (*see* Figs. 8 and 9). Most of the North Atlantic samples were taken from CSS *Hudson* in winter (January–February) and autumn (October–November) 1968. Some samples were taken from RV *Eastward*, offshore from Cape Hatteras, in November 1969, and some were taken from RV *Panulirus*, near Bermuda, in August 1968. All the South Atlantic and Pacific samples were taken from CSS *Hudson* during the *Hudson* 70 expedition. The South Atlantic samples were taken in December and January 1969–1970 (summer); the south Pacific samples were taken in April and May 1970 (autumn), and the North Pacific samples were taken in May and June 1970 (summer).

All the surface-water samples were taken from CSS *Hudson* either with a bucket or via a continuously pumped seawater sampling loop. The intake for the sampling loop was about 4 m below the waterline, but the sampling depth varied with the movement of the ship. The bucket samples were taken either from the bow with the ship moving slowly ahead or from the stern with the ship underway (usually 12–14 knots). Subsurface samples were taken with Niskin bottles (*Hudson*), with Teflon-lined Nansen bottles (*Panulirus*), or with a 200-liter Gerard-Ewing sampler (*Eastward*). Neither the size distribution nor the concentration of the suspended particulate material was affected by the method of collection. In no sample were we able to detect particle contamination.

Particle size distributions were measured with a Coulter counter (Sheldon and Parsons 1967*a*), usually within 1 hr, but always within 6 hr, of collection. Those samples not processed within about an hour (deep-water samples) were kept cool and dark. Particles with equivalent spherical diameters from 0.63 μ to about 100 μ were considered, but in many samples a smaller size range was measured. The lower limit of measurement depends to some extent on the operating conditions and also on experimental technique. The upper limit depends on the concentration of large particles in the sample (Sheldon et al. 1967).

The results are presented as smoothed size-frequency polygons (Fig. 2). The size increments (abscissa) are logarithmic and follow a series of V, $2V$, $4V$, where V is individual particle volume. These are equivalent to diameter increments of $2^{1/3}$ or $\frac{1}{3}\ \phi$ (Sheldon and Parsons 1967*a*; Sheldon

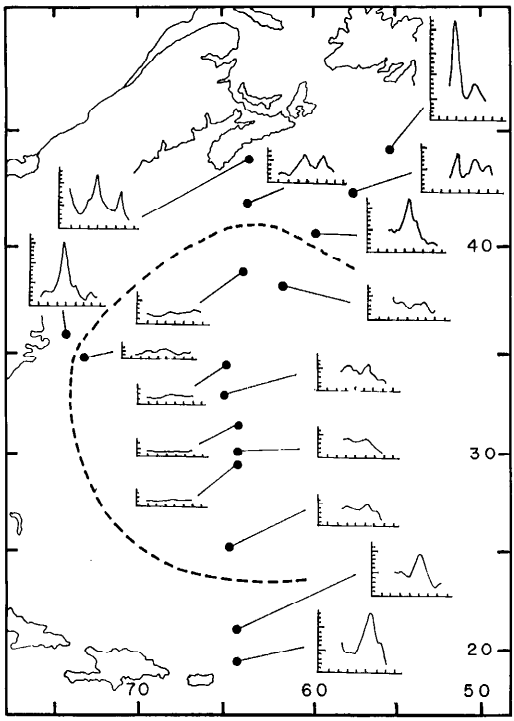

FIG. 3. Distribution of particles in the surface waters of the North Atlantic. The broken line shows the limit of the Sargasso Sea as indicated by the particle spectra.

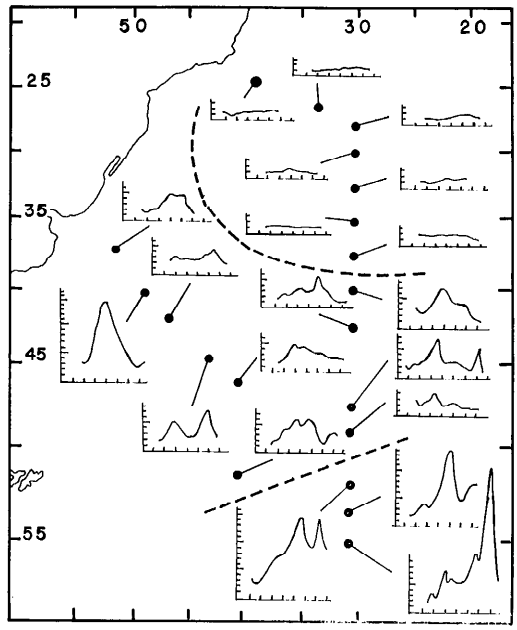

FIG. 4. Distribution of particles in the surface waters of the South Atlantic. The broken line in the north represents the limit of the subtropical water as indicated by the particle spectra. The broken line in the south represents the approximate position of the Antarctic Convergence.

1969). The ordinate represents the concentration of material in one size interval. The unit, part per million by volume, was selected because it is near to the form in which we obtain our raw data; this is equivalent to milligrams per liter if a particle density similar to that of water is assumed. We believe that this form of presentation is the best graphical method for size-frequency distributions of marine particulate material (Sheldon and Parsons 1967*b*).

GEOGRAPHIC DISTRIBUTION

The North Atlantic (Fig. 3)

In the central area, roughly between latitudes of 20° and 40°, particle concentration was low; there were approximately equal amounts of material in each size grade and there was but little variation in the form of the distributions from place to place. There was, however, evidence of seasonal variation in the total amount of particulate material present. The curves on the right-hand side of Fig. 3 (within the Sargasso Sea) are for samples taken in January. They show substantially higher concentrations than the curves on the left-hand side, which are for samples taken in November. Seasonal variation of the order shown (i.e. about a factor of 5) is not unusual for the subtropical North Atlantic (Menzel and Ryther 1960).

In more temperate waters, above about latitude 40°, the total concentration of particulate material was greater and the form of the spectra varied from place to place. The distributions still tended to have similar concentrations in each size grade but superimposed on this average level were definite, and sometimes pronounced, peaks. These peaks probably represented populations either of phytoplankton or of detrital particles.

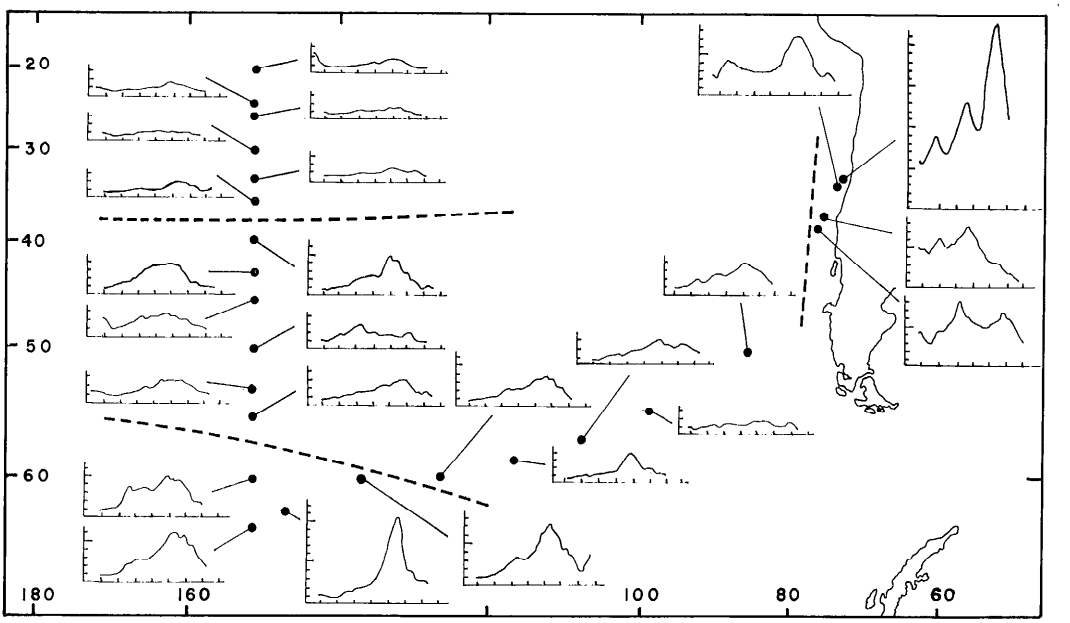

FIG. 5. Distribution of particles in the surface waters of the South Pacific. The broken line in the north represents the limit of the subtropical water as indicated by the particle spectra. The broken line in the south represents the approximate position of the Antarctic Convergence. The Chilean coastal zone is also shown (*see text*).

To the south of about latitude 25° the total concentration was also greater and the spectra showed a definite peak at around 20-μ particle diameter. This may have been caused by the nearness of the West Indian Islands, but the high standing stocks produced by the "island mass effect" tend to occur only close to the land (Doty and Oguri 1956). For instance, particle distributions near to Bermuda were typical of the Sargasso Sea and relatively high concentrations were found only within a few kilometers of the fringing reef. The relatively high concentrations found to the south of the Sargasso Sea were first encountered many kilometers to the north of Puerto Rico, and it is more likely, therefore, that they were in some way associated with the Antilles Current.

The South Atlantic (Fig. 4)

Between about latitudes 25° and 50° the South Atlantic was essentially a mirror image of the North Atlantic. The southern equivalent of the Sargasso Sea was quite clearly defined by the characteristic particle spectra, and the more temperate water to the south of about latitude 35° was also easily recognized.

To the south of about latitude 50°, beyond the Antarctic Convergence, the concentration of particles was high and relatively large particles formed the greatest bulk of material. These were mainly diatoms.

The South Pacific (Fig. 5)

The pattern of occurrence of particle size spectra was essentially similar to that of the South Atlantic, except that in the South Pacific the concentration of particles to the south of the Antarctic Convergence was rather less than we found in the South Atlantic. However, this may have been because the South Pacific samples were taken in the southern autumn. The high concentrations found near the

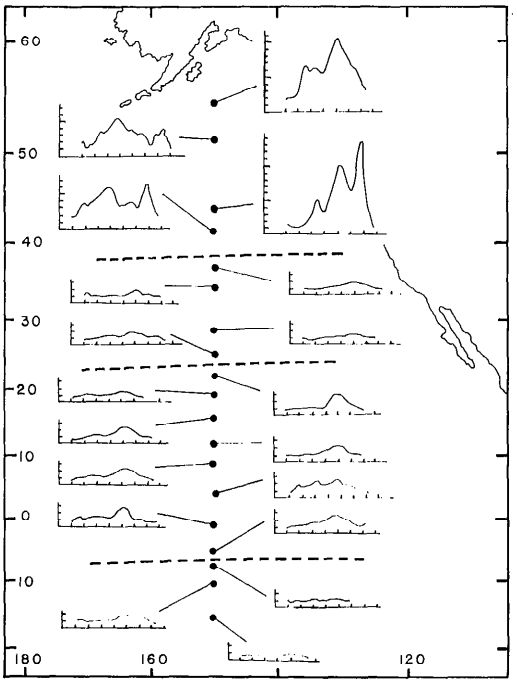

FIG. 6. Distribution of particles in the surface waters of the equatorial and North Pacific. This figure is continuous with Fig. 5 and shows, in ascending order, southern subtropical water, equatorial water, northern subtropical water, and temperate water, as indicated by the particle spectra.

Chilean coast were probably due to an effect of the Humboldt Current.

The Equatorial and North Pacific (Fig. 6)

To the south of about latitude 5°S the particle spectra were similar to those of the Sargasso Sea (*see also* the northern part of Fig. 5). Between about latitudes 5°S and 20°N the concentration of material was not great but it tended to be higher than in the subtropical area, and there was a tendency for a peak to occur at a particle diameter of about 20 μ. In the North Atlantic similar distributions were found to the south of the Sargasso Sea, although in this area the total concentration of particulate material was greater.

In the North Pacific the subtropical water with low particle concentration and particle spectra similar to the Sargasso Sea

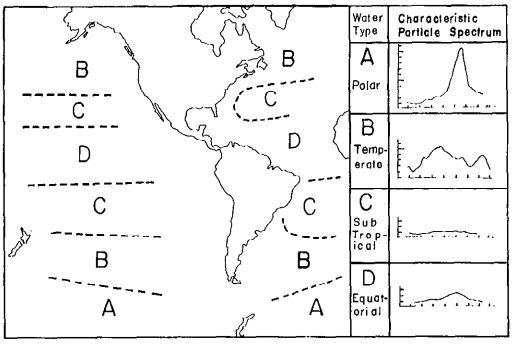

FIG. 7. Geographic pattern of particle size spectra of the surface waters.

could be recognized between about latitudes 20° and 40°. To the north of 40° high concentrations were found with large particles (diatoms) predominating in many of the samples. In other samples smaller particles were most abundant. These were probably small diatoms and flagellates. As these samples were taken during the northern summer this was not unexpected.

Summary (Fig. 7)

There were definite geographic variations in the distribution of particle size spectra, and certain areas of the ocean can be characterized simply by the size-frequency distribution of the suspended particulate material. Perhaps the clearest case is that of the subtropical areas. The roughly equal concentration of material in all size grades, together with the well-known fact of low total concentration, was first noticed in the Sargasso Sea. Subsequently, similar areas were found in the subtropical South Atlantic and in both the North and South Pacific. Particle spectra from temperate waters are also quite characteristic. Not every sample from the equatorial and polar waters was characteristic. Some of the variation could have been seasonal. However, each large area of ocean was sampled during a relatively short period and when taken as a whole the geographic pattern is fairly clear. Figure 7 represents an interpretative summary of the information contained in

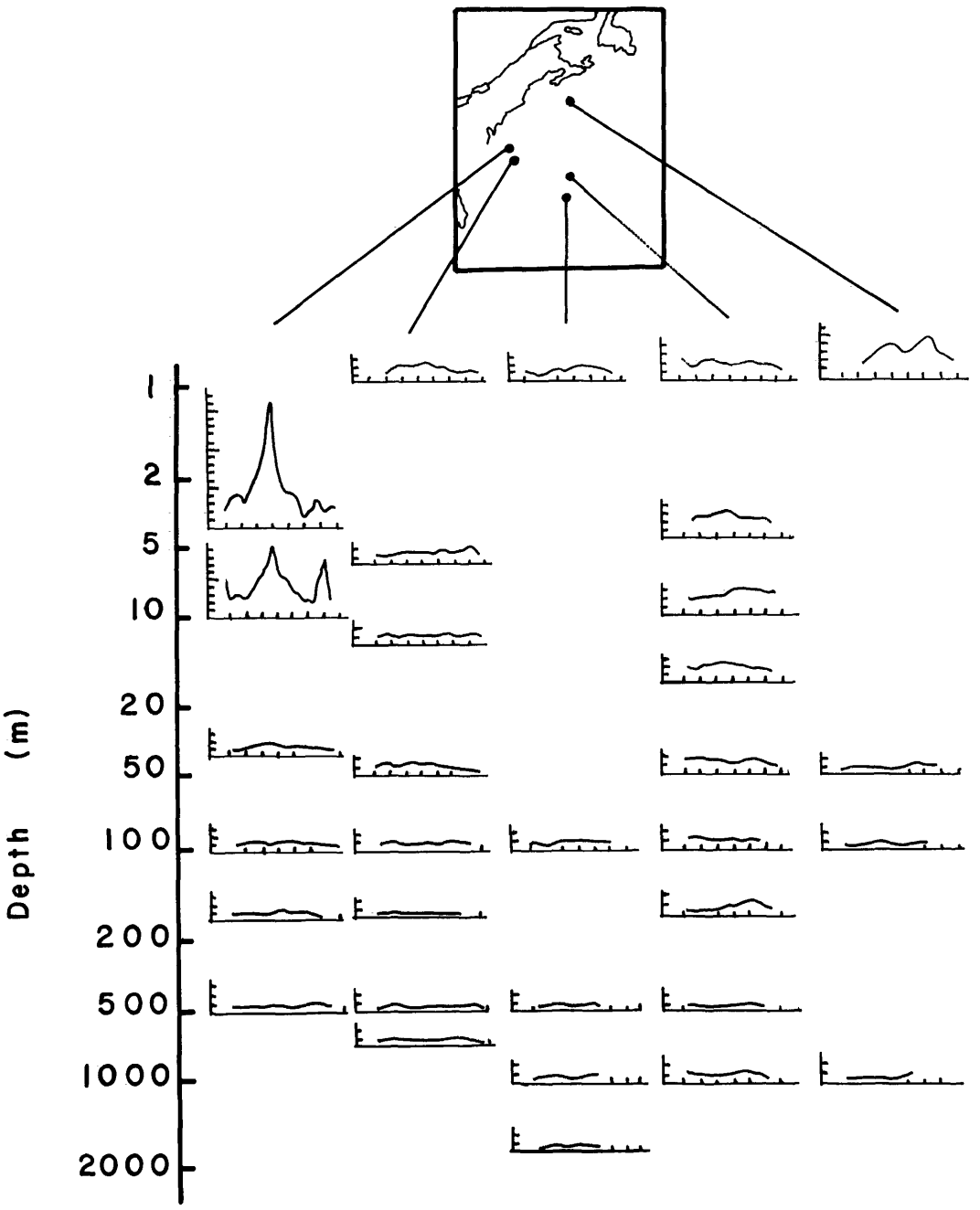

FIG. 8. Size distributions of suspended particulate matter at various depths in the western North Atlantic.

Figs. 3–6. Some parts are speculative; for instance the equatorial area of the Atlantic was defined only by two samples taken to the north of Puerto Rico, but it is clear from the evidence presented in Figs. 3–6 that the geographic pattern outlined in Fig. 7 is probably correct to a first approximation.

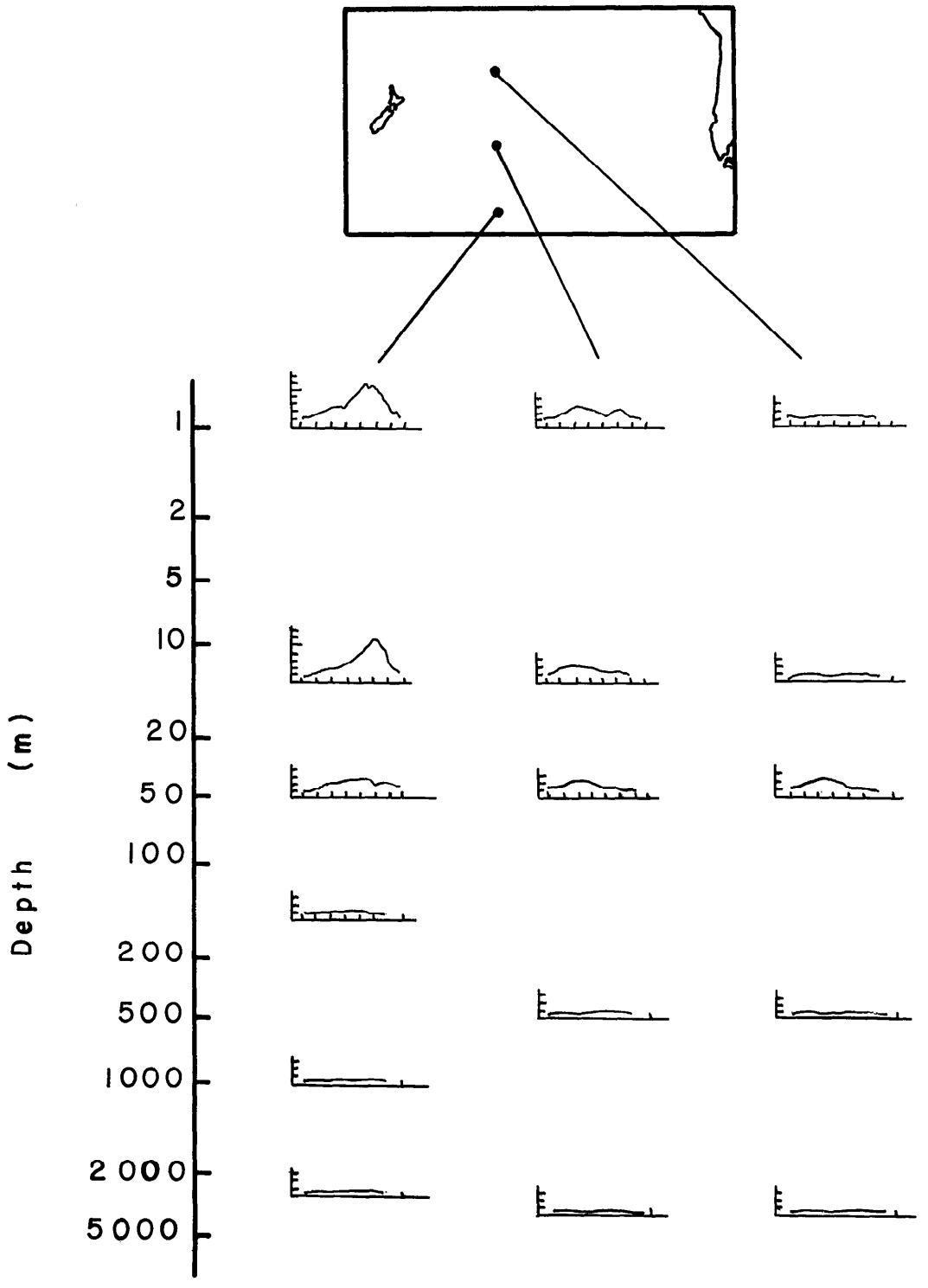

FIG. 9. Size distributions of suspended particulate matter at various depths in the South Pacific.

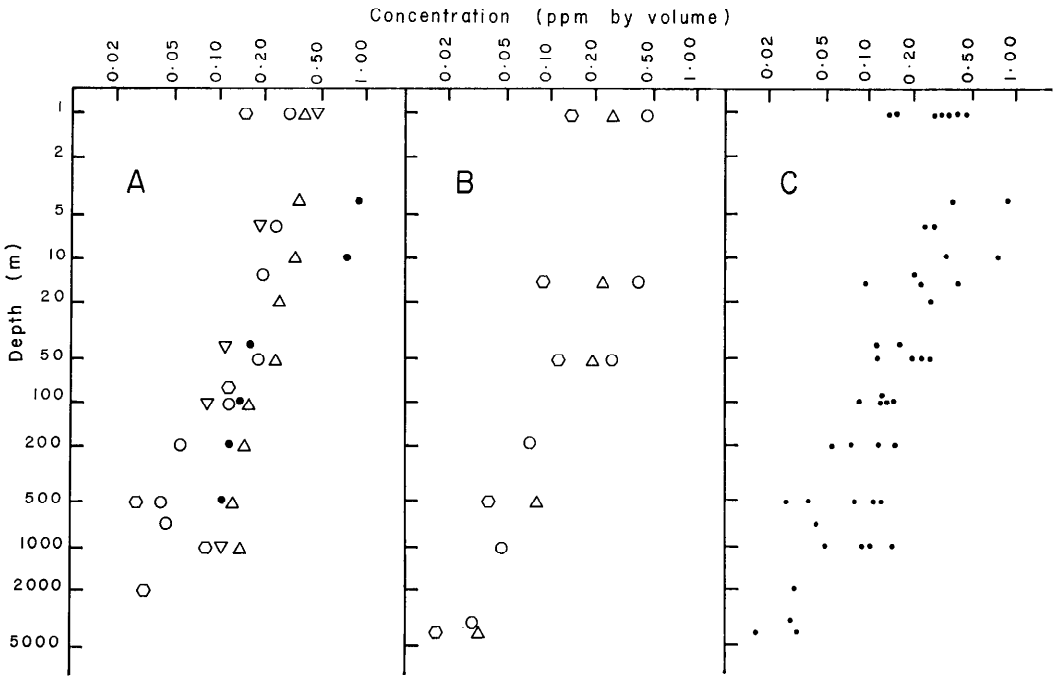

FIG. 10. Total particle concentration vs. depth. Particle size range ca. 1–100 μ.
A. The North Atlantic: ●—36° 25′ N, 74° 43.5′ W, 23–25 November 1969; ○—35° 00′ N, 73° 00′ W, 26–28 November 1969; ▽—41° 40′ N, 64° 03′ W, 29 October 1968; ○—29° 22′ N, 64° 03′ W, 2 November 1968; △—32° 18′ N, 64° 37′ W, 9–15 August 1968. These locations are shown in Fig. 8.
B. The South Pacific: ○—62° 50′ S, 149° 56′ W, 27 April 1970; △—49° 56′ S, 150° 02′ W, 1 May 1970; ○—29° 59′ S, 149° 59′ W, 7 May 1970. These locations are shown in Fig. 9.
C. Data from A and B plotted together.

DEPTH PROFILES

Samples were taken at various depths down to 2,000 m at 5 stations in the North Atlantic (Fig. 8) and to 4,200 m at 3 stations in the South Pacific (Fig. 9). The form of the particle size distributions in the surface waters varied from place to place as described above, but at depth it was remarkably uniform and resembled that of the subtropical surface water except that the total concentration of particulate material was less.

Two basically different kinds of depth profile could therefore be recognized. In the subtropical areas the particle size spectra of the surface waters showed roughly equal amounts of material in each size grade, and at depth the form of the size spectra was similar except that the concentration level was lower. In other areas there was no definite similarity between the form of the spectra at the surface and at depth.

In the deep water the *total* concentration of material was moderately variable (Fig. 10), even though the size distributions were of more or less constant form. The decrease of total concentration with depth is well known, but the depth to concentration relationship appears to be roughly log linear. It should be emphasized that these data are for concentration of particulate matter by volume in the areas we investigated. They are not therefore directly comparable with chemical data, which are given as concentration by weight, nor are they necessarily representative of the world's oceans.

DISCUSSION

Various workers have suggested that the average size of suspended particulate matter decreases with depth, and similar conclusions have been drawn both from light-scattering data and from microscopic observations (e.g. Burt 1958; Sasaki et al. 1962). Our observations, and those of Krey (1967) and Gordon (1970), seem to disagree with this, but much depends on the meaning attached to the term "average particle size." An average value can only be given to a population with finite limits. The precise definition of average is unimportant to this discussion, but it must represent some measure of a central tendency. The size distributions of particulate material in the sea, when expressed in the form we have used, are open ended. There is, therefore, no average size. As there are roughly similar *amounts* of material in logarithmically equal size intervals it follows that in any sample there will be many more small particles than large ones (Sheldon and Parsons 1967*b*). Distributions of particle number will be exponential (Beardsley et al. 1970), and the average size will be near to the smallest observable size.

Therefore, if we measure the *weight* or *volume* of material in suspension there is no average size. But if we *count* the *numbers* of particles the average size will be close to the smallest observable size.

We would suggest that average particle size apparently decreases with depth simply because, as the concentration of material decreases, the chance of finding large particles in any given sample volume also decreases. This would give an apparent increase in the relative numbers of small particles.

It is common practice to give a lower limit of particle size for the analysis of particulate material. This is usually defined in practical terms as the material retained by a specified type of filter. Not much attention has been paid to the upper size limit of the particles in a sample. If we consider a size distribution between the limits of 1 μ and 1 mm, with a constant concentration per size grade of 0.01 ppm (approximately similar to Sargasso Sea surface water), then ⅓ of the total sample will lie in the range 1–10 μ, ⅓ will be 10–100 μ, and ⅓ will be 100 μ–1 mm. However, although the sample is equally divided in terms of bulk, the number of particles per unit volume decreases rapidly as particle size increases. There will be, on average, only one particle of 100-μ diameter in 50 ml of water. A 1-liter sample would probably be representative to include this particle size. But there will be, in this example, only one particle of 1-mm diameter in 50 liter of water. A 1-liter sample would become inadequate at a particle size somewhere between these limits. That is to say, there will be inadequate numbers of particles sampled, yet the concentrations may be significant.

It has been our practice to screen samples at 160 μ. This is not really necessary for determinations of particle concentration by Coulter counter because anomalous concentrations at large particle sizes can be eliminated statistically, but for other kinds of analytical work the chance occurrence of large particles could result in anomalous determinations of particle concentration. In most surface waters 1 liter will give an adequate sample of the particles passing a 160-μ screen.

In deep water the sampling problem could be troublesome. Here the concentrations are about 10 times less than at the surface. According to our hypothesis there will be only one particle of 100-μ diameter in 500 ml of water and only one particle of 1-mm diameter in 0.5 m^3. There is clearly a need to define not only a lower limit but also an upper limit of particle size for analytical work. Sample size will then depend on the upper limit of particle size which is selected.

We measured accurately both particle size and number but we could not determine particle composition. A mineral grain and a flagellate of similar volume would be counted as similar particles. To check the nature of the suspended material we made qualitative microscopic ob-

servations on settled material whenever possible, but the inevitable difficulties associated with shipboard operation meant that not more than about 10–20% of the samples were examined in this way. However, enough samples were examined to show that, as one might expect, the suspended matter was mostly plankton and organic detritus, at least at the larger sizes. Inorganic particles not obviously associated with organisms did occur but they were not common.

Hobbie et al. (1972) have shown that in the western North Atlantic the suspended matter is mostly organic even though rather less than half of the particulate organic carbon is associated with living material (Sutcliffe et al. 1970). This does not mean that there is virtually no inorganic material in suspension. The interpretation that we place on our observations depends to some extent on the viewpoint we adopt. We consider a diatom to be a single organic particle, yet if it were analyzed chemically only a fraction of its living weight would be reported as organic carbon. Analyses are usually given in terms of dry weight, and with the data in this form the skeleton (considered to be inorganic) would make up a substantial part of the total. Therefore, when we say that most of the suspended matter is organic we do not mean that, chemically, inorganic materials are absent, but we do mean that most of the suspended matter in the ocean is associated either with nonliving organic matter or with organisms.

The tendency for roughly similar amounts of particulate material to occur in logarithmically equal size ranges has ecological implications of considerable significance. There is no reason to believe that the size range over which most of our measurements were made is atypical, except in that it was a relatively easy range to measure. Therefore, if the form of the size distributions is such that concentrations are roughly equal between 1 and 100 μ, why should not similar concentrations occur at sizes smaller than 1 μ or greater than 100 μ?

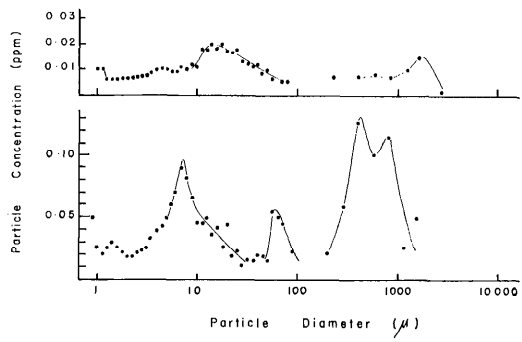

FIG. 11. Complete size spectrum over the size range 1 μ to about 4,000 μ for low and high standing stocks. Upper curve—10° 09′ S, 150° 02′ W, 18 May 1970. Lower curve—35° 00′ S, 73° 00′ W, 26–28 November 1969. Both examples from near surface water.

Particle concentrations at sizes less than 1 μ are difficult to measure accurately but we have made some observations which suggest that in the open ocean, concentrations in the size range 0.5–1 μ are not dissimilar to those in the range 1–100 μ. Quantitative observations in the size range 100–4,000 μ (zooplankton) are easier to make and in Fig. 11 we give examples at different levels of standing stock of size distributions for a range of particle size from 1 μ to about 4,000 μ. The concentrations in the zooplankton size range are similar to the concentrations in the phytoplankton size range (*see also* Harvey 1950; LeBrasseur et al. 1969; Parsons et al. 1969; Sheldon and Parsons 1967*b*).

In Fig. 12 we have attempted a synthesis of published information to establish the relationship between standing stocks of particles over a much wider size range. By considering a size range from bacteria to whales we have covered the whole of the marine food chain, more or less. In the phytoplankton and zooplankton size ranges we have used averages of our own observations. For the larger size ranges we have recalculated published information to make it roughly comparable with our data. These estimates are, of course,

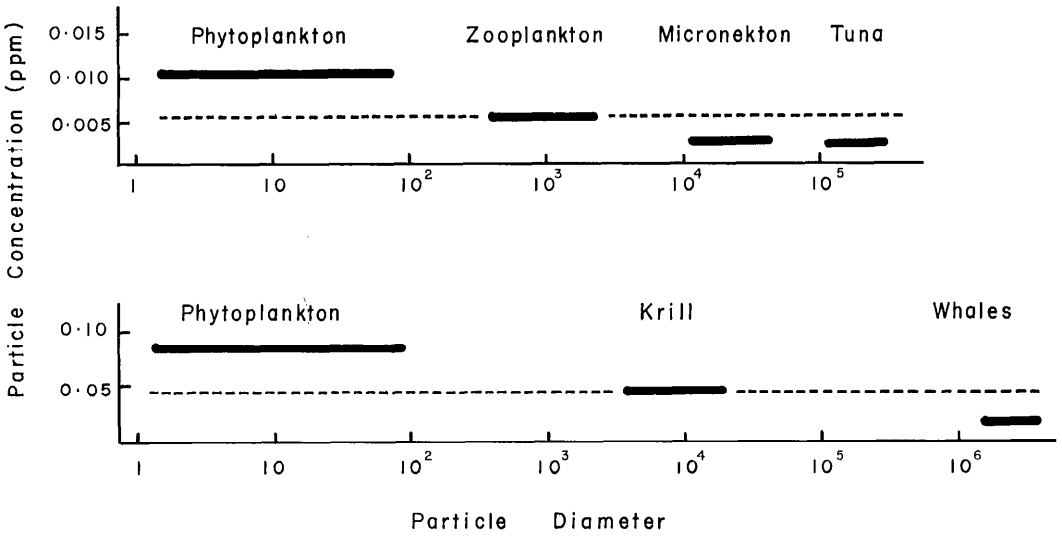

FIG. 12. Estimates of standing stock (thick lines). Above: equatorial Pacific. Below: Antarctic. The thin broken line is an estimate of the true or potential standing stock of living material. Some of the estimates were derived from data of Blackburn (1968), Blackburn et al. (1970), Mackintosh (1970), Mackintosh and Brown (1956), Marr (1962), and Riley (1963).

a first approximation only, but they are not likely to be grossly in error.

The patterns of standing stocks are similar in the two areas considered, but the absolute values differ by about a factor of 10. This is to be expected, although part of the difference may be because observations in the Antarctic were made only during the southern summer.

If we consider only the living material then the concentrations in the phytoplankton size range should be reduced by a factor of at least two (Sutcliffe et al. 1970). The zooplankton concentrations are roughly correct as it is unlikely that many nonliving particles occur in that size range. The estimated concentration of tuna (Riley 1963) probably represents a minimum for particles in its size range. The figure quoted for the concentration of whales in the Antarctic is also likely to be a minimum. The broken lines at constant concentration on Fig. 12 represent our estimates of the probable or potential standing stocks of living particles. It is unlikely that the true situation is as simple as this. Some decrease of standing stock may occur as particle size increases, but the decrease from phytoplankton to whales is probably no more than a factor of two or four, and is certainly less than an order of magnitude.

The food-chain relationships of the ocean are such that, in general, relatively large predators feed on relatively small prey. It follows from this that the pattern of standing stock that we have outlined can only be maintained if the rate of particle production varies inversely with particle size. Figure 13 shows, to a first approximation only, the relationship between rate of production (or doubling time) and particle size. There are many published data on growth, and the points and areas on the figure are only intended to be representative. Single-celled species are represented as points and other species are represented by larger areas. This is because the growth rate (or doubling time) and size of a multicellular organism varies significantly during its lifetime but a single-celled organism is less variable in this respect. The size is given as equivalent spherical diameter to be comparable

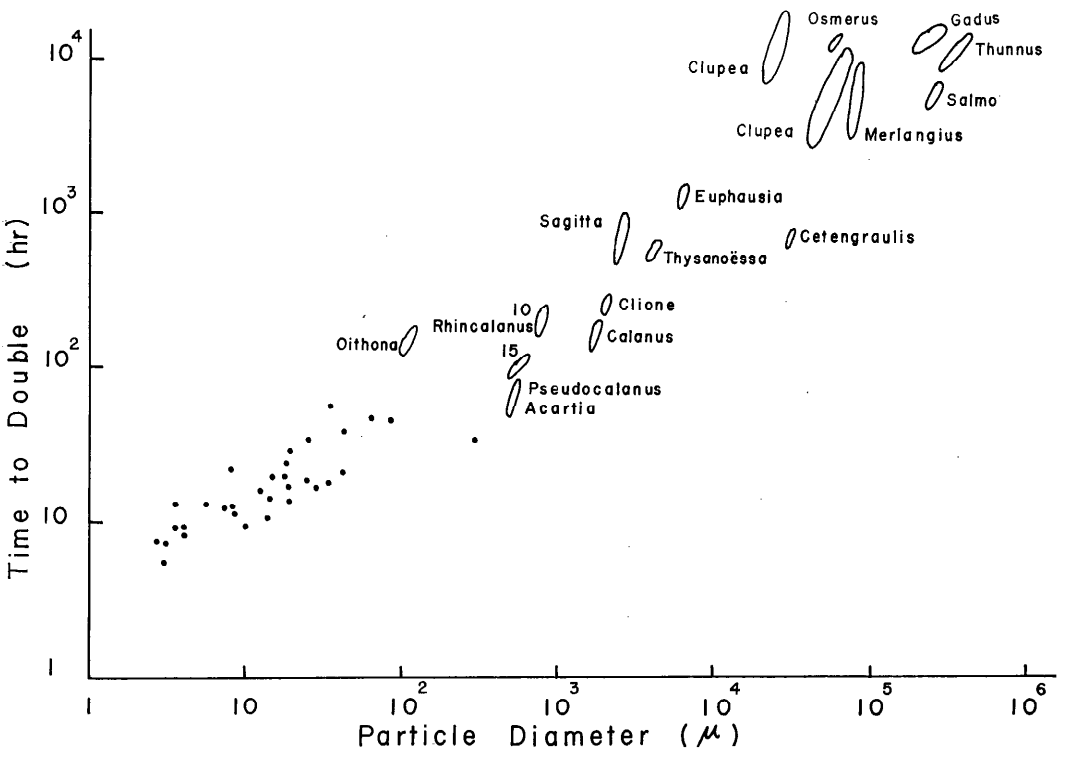

FIG. 13. The relationship between rate of production and particle size. The numbers near to the *Rhincalanus* patches indicate the temperature at which the growth took place. The uppermost of the two *Clupea* areas represents *C. sprattus*. The lower area represents both the Atlantic (*C. harengus*) and Pacific (*C. pallasi*) herring. For other explanations *see text*. Data from Altman and Dittmer (1964), Conover and Lalli (1972), Einarsson (1945), Eppley and Sloan (1966), Ford (1933), Garrod and Gambell (1965), Heinle (1966), Johnson (1970), Lebour (1925), Marshall and Orr (1955), MacLaren (1965, 1969), Mullin and Brooks (1970), Prakash (1967), Smayda (1966), and Williams (1964).

with other data in this paper; the equivalent spherical diameter of a fish varies with its shape but is about a fifth to a third the actual length. For a crustacean the spherical diameter is about half the actual length. Growth rate varies with temperature but this effect is small relative to the scale we use (*see Rhincalanus*, Fig. 13). However, the cool-water species tend to fall on the upper part of Fig. 13, indicating that at any one size, rate of production is highest in warm water.

Although for a balanced system the form of Fig. 12 predicts, qualitatively, the form of Fig. 13, and vice versa, the quantitative relationships seem to depend on subtle interactions between the growth rates and metabolic efficiencies of predators and prey. There is a need for further work to develop a sound theoretical framework, but the validity of our hypothesis can be roughly established from Fig. 13. In two well-known predator-prey links, *Clupea* to *Calanus* and *Calanus* to diatoms, rates of production vary by roughly an order of magnitude for each step. If the ecologic efficiency is about 10% then the standing stocks must be similar.

REFERENCES

ALTMAN, P. L., AND D. S. DITTMER. 1964. Biology data book. Fed. Amer. Soc. Exp. Biol. Washington. 633 p.

BEARDSLEY, G. F., JR., H. PAK, E. CARDER, AND B. LUNGREN. 1970. Light scattering and

suspended particles in the eastern equatorial Pacific Ocean. J. Geophys. Res. **75**: 2837–2845.

BLACKBURN, M. 1968. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance and relations to tuna. U.S. Fish. Wildl. Serv. Fish. Bull. 67, p. 71–115.

———, R. M. LAURS, R. W. OWEN, AND B. ZEITZSCHEL. 1970. Seasonal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. **7**: 14–31.

BURT, W. V. 1958. Selective transmission of light in tropical Pacific waters. J. Mar. Res. **5**: 51–61.

CONOVER, R. J., AND C. M. LALLI. 1972. Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. Exp. Mar. Biol. Ecol. **8**: In press.

DOTY, M. S., AND M. OGURI. 1956. The island mass effect. J. Cons., Cons. Perm. Int. Explor. Mer **22**: 33–37.

EINARSSON, H. 1945. Euphausiacea. 1. Dana Rep. 27, p. 1–185.

EPPLEY, R. W., AND P. R. SLOAN. 1966. Growth rates of marine phytoplankton: correlation with light absorption by cell chlorophyll *a*. Physiol. Plant. **19**: 47–59.

FORD, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924–1933. J. Mar. Biol. Ass. U.K. **19**: 305–384.

GARROD, D. J., AND R. GAMBELL. 1965. Whiting of the Irish Sea and the Clyde. Fish. Invest. London Ser. 2 **24**(3): 64 p.

GORDON, D. C. 1970. A microscopic study of organic particles in the North Atlantic Ocean. Deep-Sea Res. **17**: 175–185.

HARVEY, H. W. 1950. On the production of living matter in the sea off Plymouth. J. Mar. Biol. Ass. U.K. **29**: 97–137.

HEINLE, D. R. 1966. Production of a calanoid copepod *Acartia tonsa* in the Patuxent River estuary. Chesapeake Sci. **7**: 59–74.

HOBBIE, J. E., O. HOLM-HANSEN, T. T. PACKARD, L. R. POMEROY, R. W. SHELDON, J. P. THOMAS, AND W. J. WIEBE. 1972. Distribution and activity of microorganisms in ocean water. Limnol. Oceanogr. **17**(4): In press.

JERLOV, N. G. 1968. Optical oceanography. Elsevier. 194 p.

JOHNSON, P. O. 1970. The Wash sprat fishery. Fish. Invest. London Ser. 2 **26**(4): 77 p.

KREY, J. 1967. Detritus in the ocean and adjacent sea, p. 389–394. *In* G. H. Lauff [ed.], Estuaries. Amer. Ass. Advan. Sci. Publ. 83.

LEBOUR, M. V. 1925. The dinoflagellates of northern seas. Mar. Biol. Ass., Plymouth. 250 p.

LEBRASSEUR, R. J., W. E. BARRACLOUGH, O. D. KENNEDY, AND T. R. PARSONS. 1969. Production studies in the Strait of Georgia. Part 3. J. Exp. Mar. Biol. Ecol. **3**: 51–61.

MACKINTOSH, N. A. 1970. Whales and krill in the twentieth century, p. 195–212. *In* M. W. Holdgate [ed.], Antarctic ecology, v. 1. Academic.

———, AND S. G. BROWN. 1956. Preliminary estimates of the southern populations of the larger baleen whales. Norsk-Hvalfangst-Tid. **45**(9): 469–480.

MCLAREN, I. A. 1965. Some relationships between temperature and egg size, body size, development rate and fecundity of the copepod *Pseudocalanus*. Limnol. Oceanogr. **10**: 528–538.

———. 1969. Population and production ecology of zooplankton in Ogac Lake, a landlocked fjord on Baffin Island. J. Fish. Res. Bd. Can. **26**: 1485–1559.

MARR, J. 1962. The natural history and geography of the Antarctic krill. Discovery Rep. **32**: 33–464.

MARSHALL, S. M., AND A. P. ORR. 1955. The biology of a marine copepod *Calanus finmarchicus* (Gunnerus). Oliver and Boyd. 188 p.

MENZEL, D. W., AND J. H. RYTHER. 1960. The annual cycle of primary production in the Sargasso Sea off Bermuda. Deep-Sea Res. **6**: 351–367.

MULLIN, M. M. 1965. Size fractionation of particulate organic carbon in the surface waters of the Indian Ocean. Limnol. Oceanogr. **10**: 459–462.

———, AND E. R. BROOKS. 1970. Growth and metabolism of two planktonic marine copepods as influenced by temperature and type of food, p. 74–95. *In* J. H. Steele [ed.], Marine food chains. Oliver and Boyd.

PARSONS, T. R., R. J. LEBRASSEUR, J. D. FULTON, AND O. D. KENNEDY. 1969. Production studies in the Strait of Georgia. Part 2. J. Exp. Mar. Biol. Ecol. **3**: 39–50.

PRAKASH, A. 1967. Growth and toxicity of a marine dinoflagellate *Gonyaulax tamarensis*. J. Fish. Res. Bd. Can. **24**: 1589–1606.

RILEY, G. A. 1963. Theory of food chain relations in the ocean, p. 438–463. *In* M. N. Hill [ed.], The sea, v. 2. Wiley.

SAIJO, Y. 1964. Size distribution of photosynthesizing phytoplankton in the Indian Ocean. J. Oceanogr. Soc. Jap. **19**: 187–189.

SASAKI, T., N. OKAMI, G. OSHIPA, AND S. WATANABE. 1962. Studies on suspended particles in deep water. Sci. Pap. Inst. Phys. Chem. Res. (Tokyo) **56**: 77–83.

SHELDON, R. W. 1969. A universal grade scale for particulate materials. Proc. Geol. Soc. London 1659, p. 292–295.

———, T. P. T. EVELYN, AND T. R. PARSONS.

1967. On the occurrence and formation of small particles in seawater. Limnol. Oceanogr. **12**: 367–375.

———, AND T. R. PARSONS. 1967*a*. A practical manual on the use of the Coulter counter in marine science. Coulter Electronics, Toronto. 66 p.

———, AND ———. 1967*b*. A continuous size spectrum for particulate matter in the sea. J. Fish. Res. Bd. Can. **24**: 909–915.

———, AND W. H. SUTCLIFFE, JR. 1969. Retention of marine particles by screens and filters. Limnol. Oceanogr. **14**: 441–444.

SMAYDA, T. J. 1966. A quantitative analysis of the phytoplankton of the Gulf of Panama. 3. Bull. Inter-Amer. Trop. Tuna Comm. **11**(5): 355–612.

SUTCLIFFE, W. H., JR., R. W. SHELDON, AND A. PRAKASH. 1970. Certain aspects of production and standing stock of particulate matter in the surface waters of the Northwest Atlantic Ocean. J. Fish. Res. Bd. Can. **27**: 1917–1926.

WILLIAMS, R. B. 1964. Division rates of salt marsh diatoms in relation to salinity and cell size. Ecology **45**: 877–880.