

## A DISCUSSION OF SOME CRITICAL INDICES OF PRIMARY AND SECONDARY PRODUCTION FOR LARGE-SCALE OCEAN SURVEYS\*

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### INTRODUCTION

In the following presentation we have considered different types of observations which might be applied to the study of the primary and secondary production of large areas of ocean. From an initial consideration of this problem it was apparent that in order to carry out these studies a large number of ships and personnel would have to be employed for many years to come on this one facet of marine research. As an alternative, therefore, we felt that it was necessary to consider observational platforms other than research ships. Thus the type of observations that we believed would serve as critical indices of primary and secondary production have been limited by the extent to which we consider that meaningful measurements could be made from these alternative platforms. In a decreasing order of ability to cover large areas in time and space we have considered as possible platforms: satellites, aircraft, instruments towed in the surface layers by commercial shipping and simple sampling procedures carried out by fishing vessels.

One additional aid to these data gathering platforms is a fixed point in the ocean such as Ocean Weather Station "P" (50°N 145°W). It has been said that it is impossible to understand the results of a synoptic survey without having performed a time series study at a point in the area. It is equally true that a time series study is difficult to interpret without a synoptic survey of the adjacent area—the two are complementary and while we have to place certain limitations on the types of observations which may be made over large areas, virtually no limitation need be placed on the types of observations carried out from a weathership. Thus it is part of our contention that such ships should be considered an integral part of large scale oceanographic surveys and from an organizational point of view they should be considered oceanic field stations of various agencies.

Finally we have felt that in order to achieve some progress toward a solution of the problems of large scale surveys we should employ indices and models which have become well established among marine scientists as acceptable measurements and explanations of processes in the marine environment. The extension of these measurements and the use of more sophisticated models will depend greatly on the results of future basic research. For the present, however,

we have attempted to extend the use of basic concepts in order to test their validity for use in large scale studies of the ocean.

### EXPERIMENTAL

Two parameters which we have initially considered to be appropriate for large scale monitoring are stability and the penetration of light into the water column. In temperate latitudes conditions for the onset of the spring phytoplankton bloom have been shown to be largely dependent on these two variables. One approach to an examination of their effect was suggested by Gran and Braarud (1935) and developed into a prediction model by Sverdrup (1953).

The approach described by Sverdrup (1953) is based on a comparison between the depth of the mixed layer ( $D_m$ ) and the depth at which light conditions (radiation and transparency) are sufficient to allow a net increase in the primary production of a water column. The latter depth is known as the 'critical depth' and is defined as the depth above which the total production (of the water column) is equal to the total respiration. It follows that if the critical depth is greater than the depth of mixing, a net increase in production can take place. Sverdrup (1953) determined a mathematical expression for the critical depth as follows:

$$\frac{D_{cr}}{1 - e^{-k_e D_{cr}}} = \frac{I_e}{I_c k_e}$$

where  $D_{cr}$  is the critical depth in metres,  $k_e$  is the extinction coefficient ( $m^{-1}$ ),  $I_e$  is the average energy which passes the sea surface per unit time and is available for photosynthesis, and  $I_c$  is the energy at the compensation depth. (The compensation depth is defined as the depth at which the energy intensity is such that production by photosynthesis balances destruction by respiration.)  $I_e$  and  $I_c$  have been expressed in langley (ly) per hour—one langley being equal to one gram calorie per  $cm^2$ .

In using this model we have tried to accumulate data over as long a period of time as possible so as to present an average picture from which future anomalies could be judged. The following sources were used for these data:

$I_e$ , the average energy available for photosynthesis per unit time, has been determined at Station "P" from the total solar radiation measured with an Ep-

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pley pyrhelimeter. These values, averaged from January 1960 to February 1964, have been expressed as the mean hourly radiation and corrected for reflection losses by determining the mean sun altitude for each month (Sverdrup, 1953). The amount of energy available for photosynthesis has then been determined by reducing the total radiation by a factor of 0.2 to allow for absorption of non-photosynthetic energy in the first metre of sea water (Sverdrup, 1953).

For the rest of the eastern Subarctic Pacific, solar-radiation estimates computed by the U.S. Bureau of Commercial Fisheries, San Diego (Marine Weather Observation Summary for the Pacific Ocean) have been utilized. These data, which were available by 5° squares of latitude and longitude for the years 1962

through 1964, were averaged and expressed as the hourly photosynthetic radiation, corrected for cloud cover and for reflection, for each month.

Estimates of the depth of the mixed layer ( $D_m$ ) during February have been taken from Giovando and Robinson (1966). For the areas 55–60°N, 150–160°W, and 40–45°N, 150–160°W, where no statistical estimation of the depth for the mixed layer has been made by these authors, an approximation of the mean mixed-layer depth plus or minus one standard deviation has been made from bathythermograph data (available at the Pacific Oceanographic Group, Nanaimo) for January to April during the years 1957 and 1962 through 1964. Data on the mixed-layer depth obtained by Giovando and Robinson (1966)

CRITICAL DEPTHS AND DEPTH OF MIXING AT STATION P

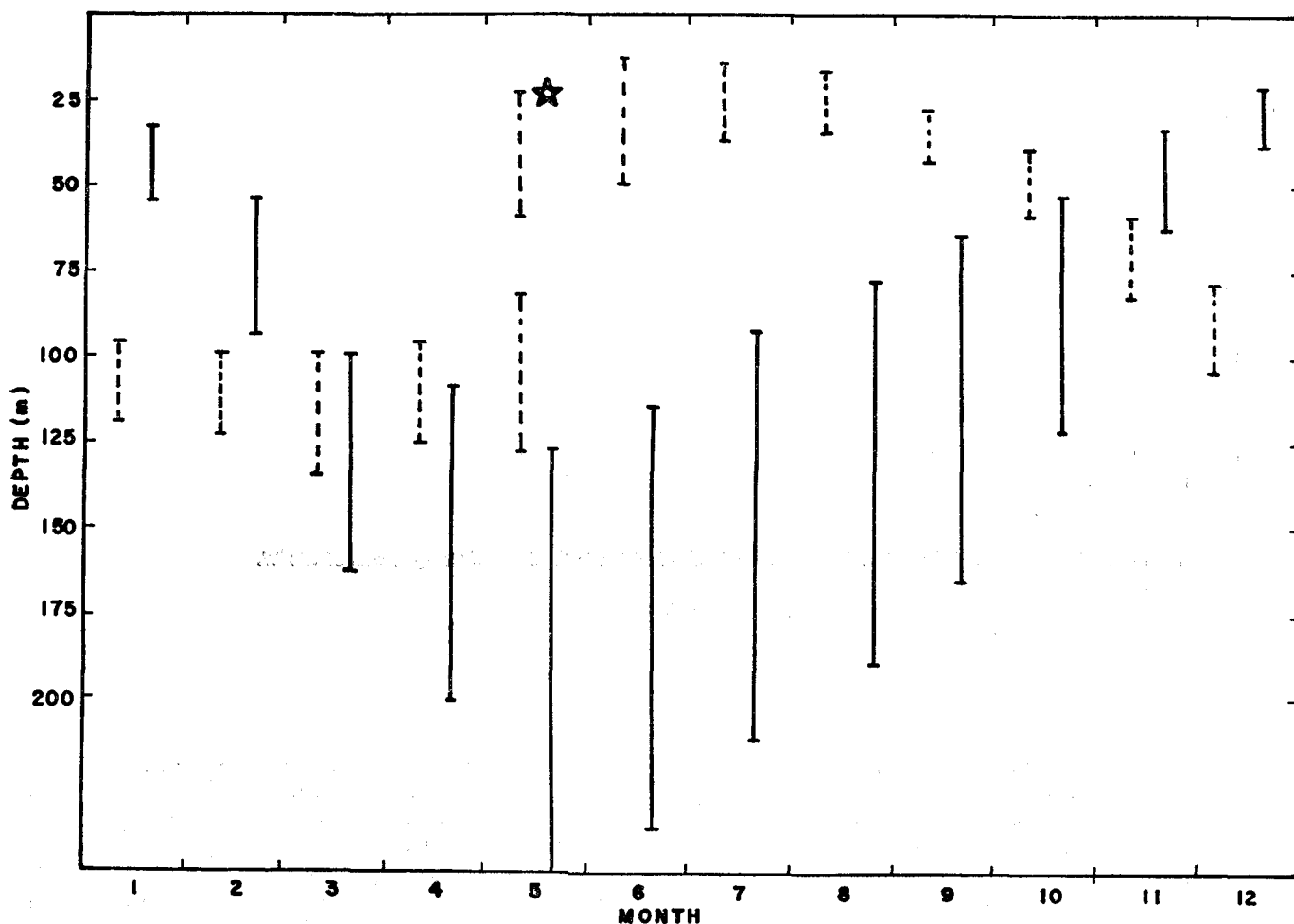


Figure 1. A comparison of the critical depth and the depth of mixing at Ocean Weather Station "P"

Legend: Maximum and minimum critical depth

Approximate mean mixed layer depth, plus or minus one standard deviation (data from 1947–1963)

\* During the years 1956–59, 1962–63 the "new" seasonal thermocline was formed near the middle of May.

CRITICAL DEPTHS AND DEPTH OF MIXING IN THE  
STRAIT OF GEORGIA, WEST OF 124° W.

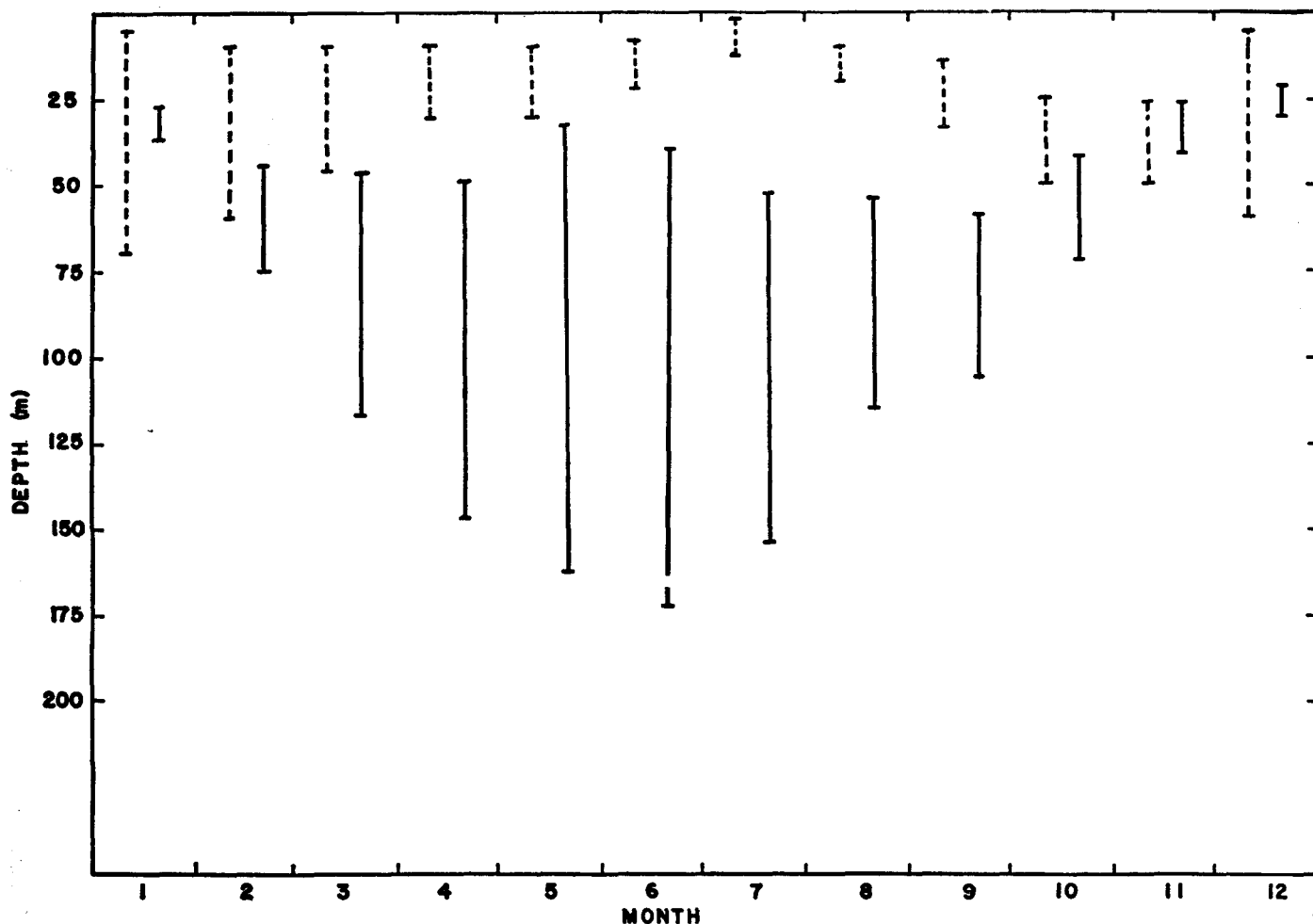
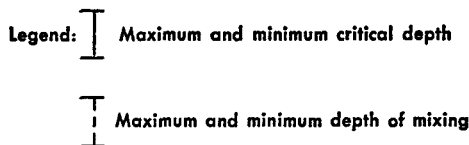


Figure 2. A comparison of the critical depth and the depth of mixing in the Strait of Georgia, west of 124°W.



have been represented in Fig. 1 for each month of the year at Station "P". In Figure 4 are shown values of the mixed-layer depth from north to south along lines of longitude, at 10° intervals, from 125° to 155°W. In this manner, estimates of the critical depth, which were made by 5° intervals of latitude and 10° intervals of longitude, can be compared with estimates of the mixed-layer depth which have been reported by areas composed of 5° intervals of latitude and 2° intervals of longitude, (Giovando and Robinson, 1966). In reporting the latter results, where two areas of latitude and longitude are adjacent (east and west of a line of longitude), the larger maximum and the smaller minimum values for the mixed-layer depth have been entered in Fig. 4.

The extinction coefficient,  $k_e$  ( $m^{-1}$ ), has been expressed as maximum and minimum values for each month from Secchi disc data accumulated during 1957 through 1962 at Station "P" (Parsons, 1965). These values have been expressed as extinction coefficients for blue light which have been derived from the formula given by Poole and Atkins (1929):

$$k_e = \frac{1.7}{D}$$

where D is the Secchi disc depth in metres. For the remainder of the eastern Subarctic Pacific, Utterback and Jorgensen's (1934) oceanic-average extinction for

the area,  $0.073 \text{ m}^{-1}$  at 4800 Å, has been employed. This value is representative of minimum extinction values at Station "P" during the spring. Maximum extinctions during the spring at Station "P" also have been included in calculations of the critical depth in the remainder of the northeast Pacific by using the maximum extinction for March of  $0.13 \text{ m}^{-1}$  (Parsons, 1965).

The value used by Sverdrup (1953) for  $I_c$ , the energy at the compensation depth, was taken from Jenkin (1937) as being 0.13 ly/hr. This value was determined for a day length of 16 hours, which sug-

gests that a slightly larger value might be considered for the spring when the day length is less. However, in the absence of sufficient information on the effect of light and dark periods on the compensation light intensity, the value of 0.13 ly/hr has been employed here for purposes of comparability with other authors (Marshall, 1958, Sverdrup, 1953 and Cushing, 1962).

Copepod weights used in this presentation are from data accumulated by LeBrasseur (1965 and 1966). Collections were made with a standard North Pacific net hauled vertically from 150 m to the surface.

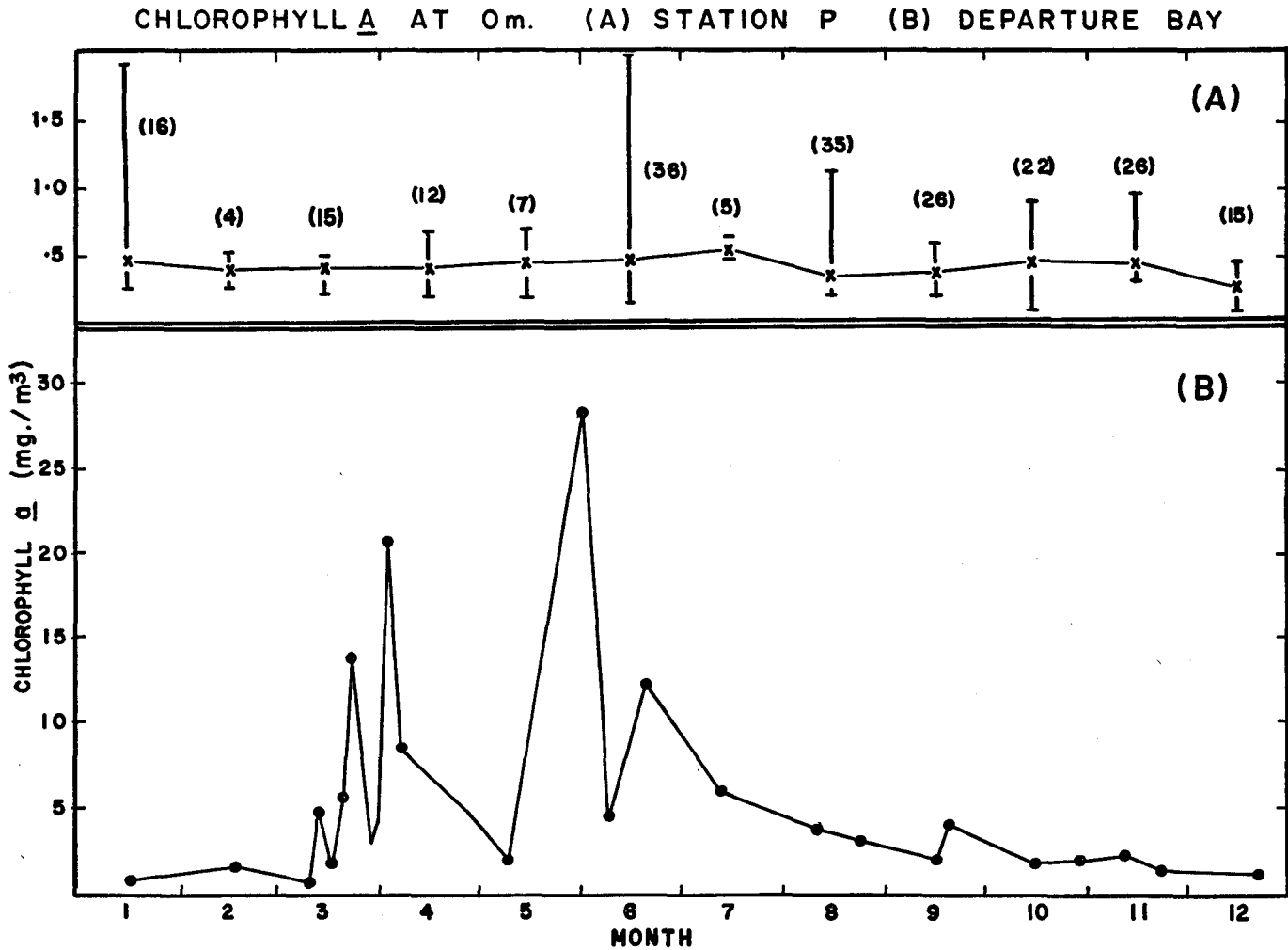


Figure 3. Surface chlorophyll a values at Station "P" and in Departure Bay. Legend: Station "P"; average values, x; number of determinations, 1958 to 1964, (25); maximum and minimum values represented as bars. Departure Bay; data from Parsons (1960)

DISCUSSION OF FIGURES 1 TO 6

Figure 1

In this figure the range of maximum to minimum critical depths at Station "P" in each month of the year is shown as solid bars. The depths of mixing, plus or minus one standard deviation, are shown as dotted lines. Two depths of mixing are shown for the month of May since the "new" seasonal thermo-

cline in some years is established in this month rather than June.

From this figure it may be seen that during the period December to February the maximum critical depth is less than the minimum depth of mixing. This would indicate that there could be no net increase in primary production at Station "P" during this period. On the other hand, from May through September the minimum critical depth is equal to or

greater than the maximum depth of mixing, indicating that this is the principal period in which a net increase in primary production can occur. For the months of March and April, and again in October and November, conditions are such as to permit some increase in net production under favorable conditions. It appears therefore that for the advent of the spring bloom, the months of March and April will be the most important in determining the timing of this event.

### Figure 2

Data are shown here on the mixed-layer depth and the critical depth for each month of the year in a coastal region at the same latitude as Station "P". It may be seen that in contrast to Station "P" the much higher stability, due to freshwater runoff in this area, has allowed conditions to develop so that a net increase in primary production would be expected during March. Further it appears that throughout the winter some production could occur in this area providing relatively stable conditions and/or a suit-

able degree of transparency were maintained for a sufficient period of time. To approach a plankton bloom, however, assuming a maximum generation time of 48 hours for winter radiation levels, suitable conditions would have to be maintained for about two weeks. This period is considerably longer than is generally encountered during the winter in the Strait of Georgia.

### Figure 3

Data are shown here on the seasonal variation in the surface concentration of chlorophyll *a*/m<sup>3</sup> at Station "P" and at Departure Bay in the Strait of Georgia. The latter values, collected during 1958-1959 show that a marked increase in the standing stock of phytoplankton occurs during March which is in agreement with the prediction shown in Figure 2. At ocean Station "P", however, average concentrations of chlorophyll *a* show little change with season. There is good evidence that this absence of a marked change is due to intensive zooplankton grazing (McAllister *et al*, 1960) which must commence

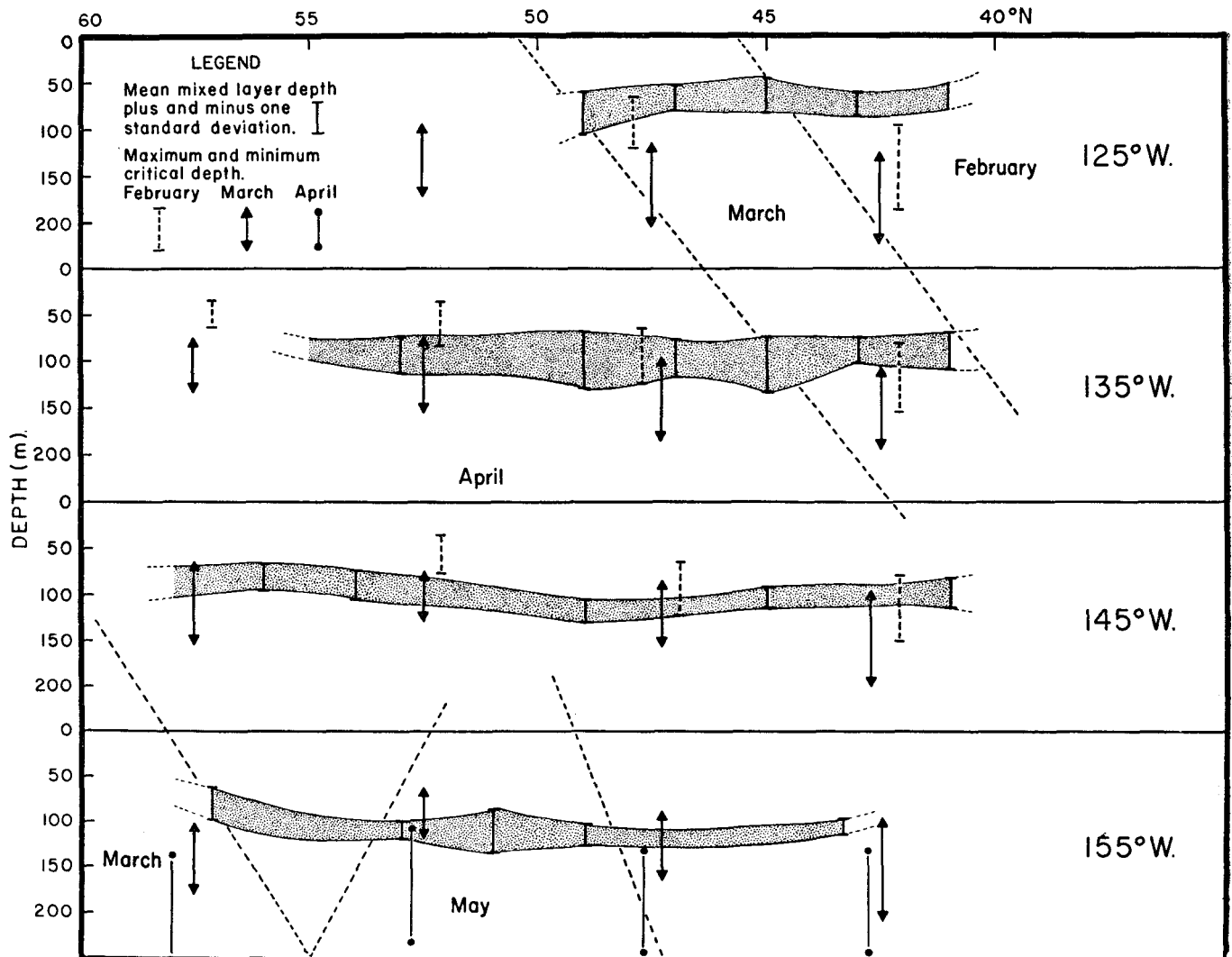


Figure 4. A comparison of critical depths and the depth of mixing in the eastern Subarctic Pacific Ocean, February to April.

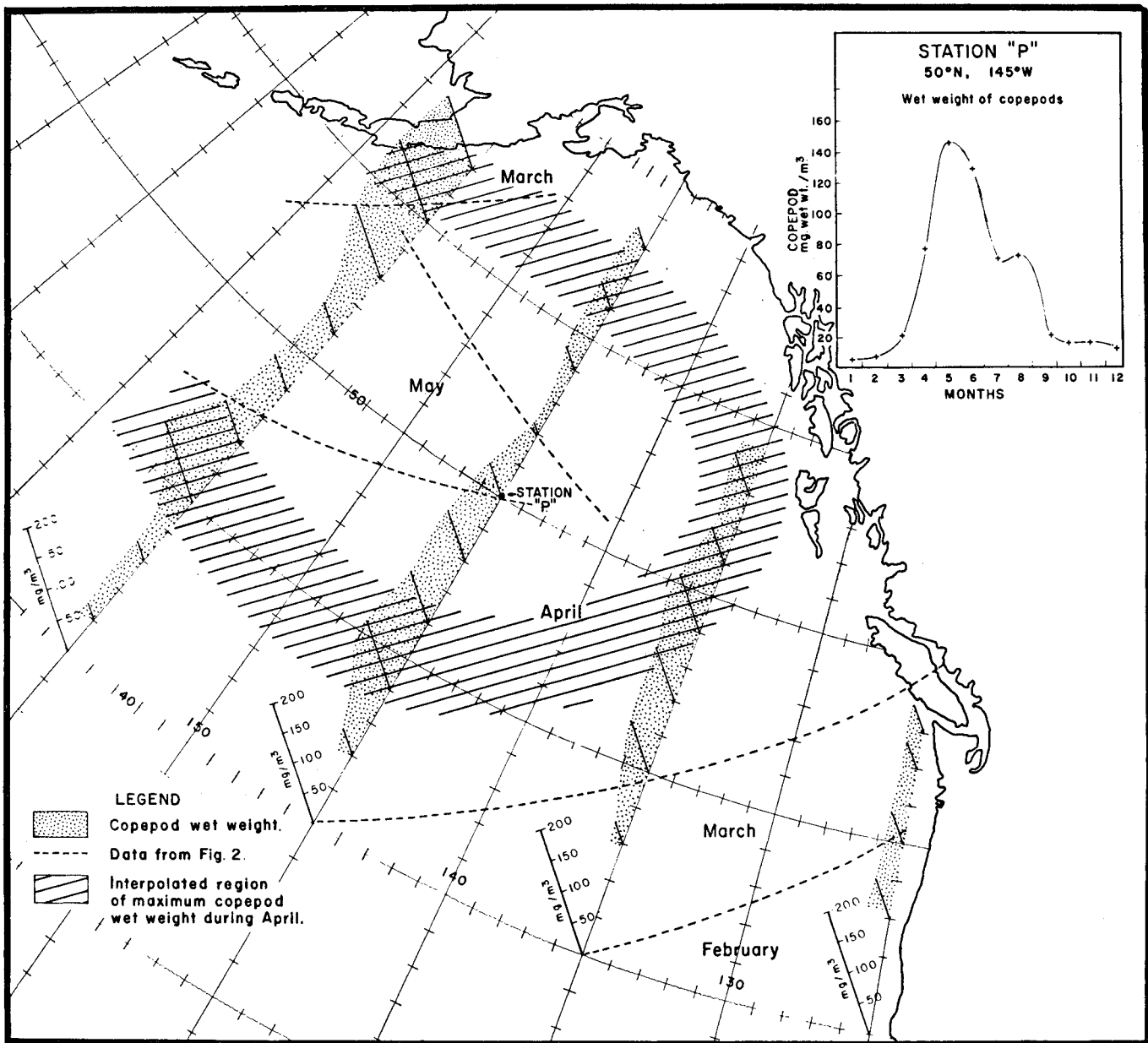


Figure 5. A comparison of copepod wet weights during April and the occurrence of the spring phytoplankton bloom in the eastern Subarctic Pacific Ocean, February to May.

simultaneously with a net increase in the primary production during the spring. (Another example of this suppression of changes in the concentration of phytoplankton is discussed by Heinrich, 1962).

**Figure 4**

In this figure we have confined the reported data to the mixed-layer depth and the critical depth during February, March and April, but extended the area of observations from 40 to 60°N and by lines of longitude at 10° intervals from 125 to 155°W. The mixed-layer depths are shown as solid bars and are joined by the shaded portion.

Critical depths are shown for February as broken bars and if we take as a criterion of timing the

month in which the minimum critical depth is greater than the maximum depth of mixing, then only at 125°W between 40 and 45°N are conditions firmly established for a net increase in primary production during February.

During March, the minimum critical depth is greater than the depth of mixing up to 50°N at 125°W and out to 135°W at 40°N. Another small area exists at this time at 155°W and 55 to 60°N.

For simplification of the figure the only April critical depths shown are along the 155°W line. In the rest of the area, except at Station "P" (Figure 1), the April minimum critical depth is below the depth of mixing. The only other exception is in the central

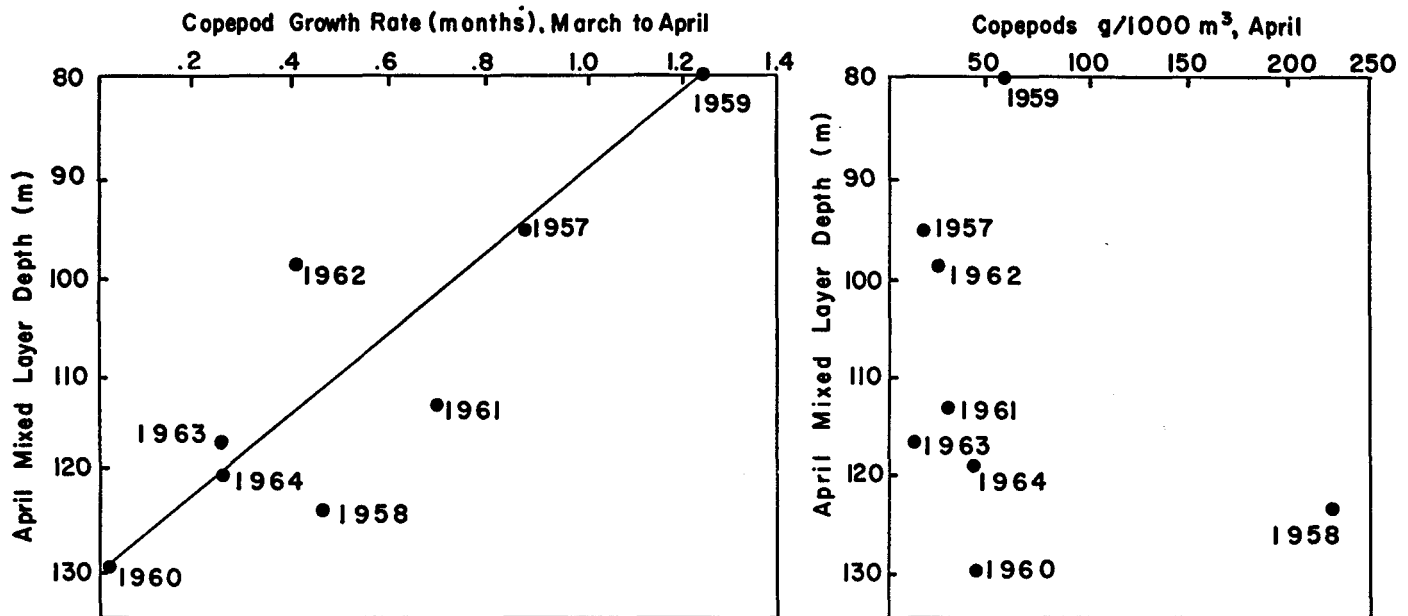


Figure 6. A comparison of the mixed layer depth at Station "P" and the growth rate of copepods (left); (right) the standing stock of copepods. Data from 1957 to 1964.

part of 155°W where the minimum critical depth does not exceed the depth of mixing until May.

Lines drawn diagonally across this figure separate, by month, areas in which hydrographic and radiation conditions are such as to firmly establish conditions for a net increase in primary production. These lines have been transposed to the next figure.

#### Figure 5

Dotted lines drawn on Fig. 4 which separate areas in which conditions for a net increase in primary production become established in the same month, are compared in this figure to the average copepod wet weight for the month of April. An area of approximate copepod maxima has been drawn in as an interpolation of the results of copepod wet weights shown in this figure. From a comparison of these results it may be seen that maximum copepod weights are encountered in areas north and south of Station "P", in a semicircle approximating the areas in which a net increase in primary production occurs during March to April. Minimum copepod weights are encountered in a central portion of the northeast Pacific between a wide area at 155°W and a narrower area extending east beyond Station "P". This area of low copepod weight approximates the area in which conditions for a net increase in primary production are not firmly established until May. These results are further substantiated by the inset to Fig. 5 which shows that maximum copepod biomass at Station "P" does not occur until the period May to June.

Other evidence supporting the description of the spring bloom discussed here can be found in primary production data for Station "P" (McAllister, 1962). These data show values of up to 1100 mg C/m<sup>2</sup>/day

during the period May-June compared with values of 200 or less mg C/m<sup>2</sup>/day during March-April. From data reported by Stefansson and Richards (1964) it is apparent that in the area of 40-45°N and 125-130°W, nitrate depletion starts in February and that the nutrient becomes exhausted from the surface layers by May. These results are also in keeping with the sequence of events shown in Figs. 4 and 5.

There are, however, some inconsistencies in Fig. 5 in that the central copepod minimum at 155°W is greater than some of the maxima at 145°W. This may be partly explained if we were to consider that there are other effects of the environment, such as currents, which determine the actual numbers of copepods present. An alternate and possibly more plausible explanation is that the critical-depth model does not predict the total biomass but only growth-rate of copepods in this area.

This may be demonstrated in the following manner: The species of copepod primarily responsible for the increase during the spring is *Calanus plumchrus* (generally from 40 to 90% of the biomass). Further it is widely distributed during March and April, and as spring progresses the increase in copepod biomass is in a large part due to this animal getting fatter and changing from Stage IV to V. Thus if, on the inset to Fig. 5, the exponential increase in copepod biomass is taken as an approximation of growth-rate during March and April at Station "P", then this value in different years should be predictable from the ratio of  $D_{cr}/D_m$ .

#### Figure 6

In this figure the measure of copepod growth-rate ( $\log_{10}$  biomass in April minus  $\log_{10}$  biomass in March divided by the time-interval in months) has

been plotted against the depth of the mixed layer from 1957-1964. Radiation data are not available for the same period so that we have had to leave out half of the model ( $D_c$ ) in plotting the ordinate. The indication is still clear, however, that there is a measure of growth-rate which is related to the mixed-layer depth; but that, as is shown in the second part of the figure, there is no apparent relationship between the standing stock of copepods and the mixed-layer depth. Thus it is apparent that the model gives some measure of growth-rate but not of recruitment of copepods.

### Conclusions from Figures 1 to 6

In conclusion to this first part of our presentation we feel that we can now at least partially answer Dr. Stewart's question when he asked earlier, what types of data does the biologist want collected for large scale oceanic studies? If we return to the right hand side of the equation for the Sverdrup model, then we want an improvement in the collection with time, by area and in accuracy of the three terms,  $I_e$ ,  $k_e$ , and  $I_c$ .  $I_e$ , the effective photosynthetic radiation, should be monitored over the northern (north of about 40°N) hemisphere and, initially at least, reported as a monthly average for each 5° square. This value could be improved in accuracy by correcting for reflection due to the effect of wind on the sea surface and by an accurate measure of the energy in the photosynthetic portion of the spectrum. The extinction coefficient,  $k_e$ , should also be routinely measured over the same area and it is suggested that some kind of disposable light meter for use with aircraft might greatly assist in the collection of these data. Our knowledge of  $I_c$ , the compensation light-intensity, might be initially improved by laboratory studies but field investigation of this value from research ships would ultimately be desirable.

Also inherent in the model is the continued collection and improved coverage of data on the mixed-layer depth,  $D_m$ .

Finally, while three of the above terms can probably be best collected from satellites or aircraft, the actual biological data with which the model can be correlated should also be routinely collected. As has already been mentioned in the introduction, these data (e.g. chlorophyll  $a$ , primary production, zooplankton biomass) are probably best collected from commercial shipping or from fishing boats in the area.

So far we have been discussing essentially the timing of events in the N.E. Pacific Ocean and their relation to the rate of increase of primary and secondary producers. Looking at a different aspect of this problem it is possible to divide up the effects of stability and radiation on the production of a water column and compare these effects at different latitudes and in different oceans. As in the previous study, the quantity and time at which data have been collected permit only a broad assessment of this problem but we believe that the following discussion gives

a good appraisal of the effect of stability and radiation on primary production.

Table I shows the effect of increased radiation, February to May, on the growth-constant of a chrysophyte. The actual production at Station "P" (line 1) has been taken as representative data from McAllister (1962) as reported by Parsons (1965). Average photosynthetic-radiation data measured with a pyrhelimeter at Station "P" is reported in the second line (Parsons, 1965). In the third line the effect of this increase in radiation on the growth constant of *Monochrysis lutheri* has been determined from data given by McAllister, *et al.*, (1964). This organism was chosen since it is a chrysophyte and most of the crop at Station "P" is believed to be coccolithophores. It is also the only rate-versus-light intensity curve we could find in which the study had been carried out over a sufficient period of time to reflect the true growth-response of a chrysophyte to light-intensity rather than the adaptive response of organisms taken from one light-intensity and incubated for a short period of time in a light-intensity gradient. Finally in line 4 of Table I the increase in growth-constant for March, April and May is represented as a multiple of the growth-constant in February.

TABLE I  
INCREASE IN PRIMARY PRODUCTION DUE TO  
RADIATION AT STATION "P"

	February	March	April	May
1. Approximate average production (1959-1961) mgC/m <sup>2</sup> /day.....	25	75	220	500
2. Radiation (PAR) ly/hour (1960-1964)...	0.82	1.56	2.12	2.94
3. Growth constant for <i>M. lutheri</i> using radiation values (2) above.....	.008	.02	.04	.05
4. Increase in production from (3) above...	--	X2.5	X5	X6.2

\* Data from McAllister, C.D., N. Shah and J.D.H. Strickland. J. Fish. Res. Bd. Canada 21: 159-181, 1964.  
PAR, photosynthetically active radiation.

TABLE II  
INCREASE IN PRIMARY PRODUCTION DUE TO  
STABILITY AT STATION "P"

	February	March	April	May
1. Average mixed layer depth (m) (1959-61)	113	128	101	68
2. Compensation depth (m) (1960-64) ( $k_e = 0.075$ ).....	25	33	37	42
3. $D_c/D_m$ .....	.22	.26	.36	.62
4. Increase in production from (3) above...	--	X1.2	X1.6	X2.8

In Table II the mean mixed-layer depth at Station "P", February to May has been reported from Robertson *et al.*, (1965). In line 2 the compensation depth at Station "P" has been calculated from the radiation data in Table I, assuming an average extinction-coefficient of 0.075. The effect of stability on the com-



compensation depth has been determined in the third line by taking the ratio of the compensation depth and the depth of mixing. The increase in this ratio for the months of March, April and May as compared with February is shown in the last line.

Although the major effect in increasing the ratio  $D_c/D_m$  from February to April is due to the increase in  $D_c$ , the effect of an increase in  $D_c$  is only made possible during this period by the relative constancy of  $D_m$ . Thus while  $D_c$  is a function of radiation, the efficacy of the compensation depth is determined by the stability of the water column which is quite different from the effect of increased radiation being considered in Table I.

TABLE III  
TOTAL EFFECT OF CHANGES IN RADIATION AND STABILITY  
ON PRIMARY PRODUCTION AT STATION "P"

	February	March	April	May
1. Approximate average production (1959-1961) mgC/m <sup>2</sup> /day-----	25	75	220	500
2. Increase in production compared with February-----	--	X3	X8.8	X20
3. Increase due to radiation (Table I)-----	--	X2.5	X5	X6
4. Increase due to stability (Table II)-----	--	X1.2	X1.6	X2.8
5. Total effect of radiation and stability---	--	X3	X8	X17

Table III provides a summary of data in Tables I and II and a comparison of the effects of radiation and stability on the actual increase in primary production. Thus the initial increase in production during March at Station "P" is primarily due to the effect of increased radiation on the growth-rate of the primary producers. This is also true for April but a larger proportion of the increased production in this month is due to stability. From April to May there is little effect of increased radiation on the growth rate of individual cells but there is a marked increase in the production of the water column due to stability. Finally the total effects of radiation and stability at Ocean Station "P" show that the increase in radiation on the growth-rate of the phytoplankton is about twice that of the increase in production due to stability. Further these combined effects (line 5) are in quite good agreement with actual increase in primary production at Station "P" (line 2).

While at Station "P" radiation apparently determines the increase in growth-rate as well as to a large extent the increase in stability (through the formation of the seasonal thermocline) in other areas these effects assume a different proportion. Thus from Marshall's (1958) studies in the Arctic it is apparent that a shallow mixed-layer is strongly maintained during the spring by a salinity gradient and the effect of increased radiation on production is much greater than further south in the Atlantic where the winter mixed-layer depth extends to 200 m. In the northern Sargasso Sea, however, there is sufficient radiation

throughout the year for production, but the stability of the water column is believed to limit production during a few months of the year (Riley 1957). A similar discussion of these changes from north to south in the Atlantic may be found in Cushing (1962).

Finally there appears to be a marked difference in the onset of the spring bloom in the North Atlantic and Pacific Oceans. Throughout the subarctic water mass in the Gulf of Alaska a halocline at about 100 m exists throughout the year. Thus even in the absence of a seasonal thermocline at some shallower depth, conditions for a net increase in the production of the water column are firmly established by May (Fig. 1). The productive column is relatively shallow, however, being limited by the halocline at ca 100 m. In the North Atlantic the mixed-layer depth, at the same latitudes and off the continental shelf, extends to 200 m during the winter. Under the latter conditions the onset of the spring bloom is more dependent on the formation of the seasonal thermocline. Thus primary production during the spring in the North Atlantic will tend to start later but develop more rapidly than in the North Pacific. One possible explanation, therefore, for the lack of synchronization between the phytoplankton bloom and the zooplankton crop in the North Atlantic is that the phytoplankton are produced initially in the spring at a greater rate than can be grazed by the zooplankton. In the North Pacific, on the other hand, the mean generation rate of the phytoplankton in the water column must be equal to the grazing rate of the zooplankton. The difference in the species of secondary producers has also been given as another possible explanation for the differences in the spring bloom in these two oceans (Banse, 1964). It is probable in fact that both the relative stability of the environment and the grazing patterns of the zooplankton play a role in determining the extent of the spring phytoplankton bloom in each ocean. It is imperative, however, that for a study of the former effect there should be an improvement in the large scale collection of the types of data discussed in the first part of this presentation.

To conclude it is perhaps worth considering the extent of variations within small areas of ocean. So far in this discussion we have been considering a unit area of about a 5° square of latitude and longitude and a time period of one month. From studies on surface pigment-concentrations in the Gulf of Alaska (Parsons, 1965) it is apparent that the range of variation of chlorophyll *a* in 5° squares regardless of season is about 0.2 to 0.8 mg/m<sup>3</sup>. A similar order of variation can be found during a time interval of one day in a seven mile-square in the same region (Antia *et al*, 1962). Thus, while we have shown in Fig. 3 that the monthly-mean surface-chlorophyll *a* concentration at Station "P" remains virtually constant, small variations in time and space occur which may provide an insight into local production processes or grazing patterns. These sub-area variations must be studied with different techniques than those suggested in the first part of this presentation and the

development of a variety of automated recorders for measuring nutrients, particulate material and zooplankton are particularly desirable for these studies.

## DISCUSSION

*Smith:* Were there other measurements of non-conservative properties on this fine-scale sampling pattern?

*Parsons:* When we carried out the study on the distribution of chlorophyll *a* within a seven-mile square the only other measurements made were for salinity and silicate. Since neither of these parameters reflected the same degree of variation as the chlorophyll *a* data, we felt that the latter might be a result of zooplankton grazing patterns. No environmental evidence was obtained, however, for this suggestion.

*McGowan:* What proportion of the standing crop of zooplankton is made up of grazers in your study area?

*Parsons:* The data which I have reported in the previous figures are for copepod biomass. Assuming that the copepods were the only grazers, then the proportion of these animals was about 90% of the total zooplankton standing stock.

*Schaefer:* It has been suggested (by Banse?) that differences in seasonal phytoplankton between open North Pacific and open North Atlantic, north of about 45°N, are due to differences in the life cycle of major zooplankton forms. The egg production of *Calanus* sp. in the North Atlantic is directly related to availability of food and commences only in spring. The two dominant Pacific *Calanus* species produce eggs from reserve materials, independent of phytoplankton concentration. Because of reproduction in winter, the offspring of the Pacific forms may prevent the spring bloom.

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