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Proceedings of the Conference on

PRIMARY PRODUCTIVITY MEASUREMENT, Marine and Freshwater

held at
University of Hawaii
August 21 - September 6, 1961

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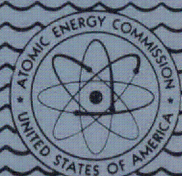

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Biology and Medicine

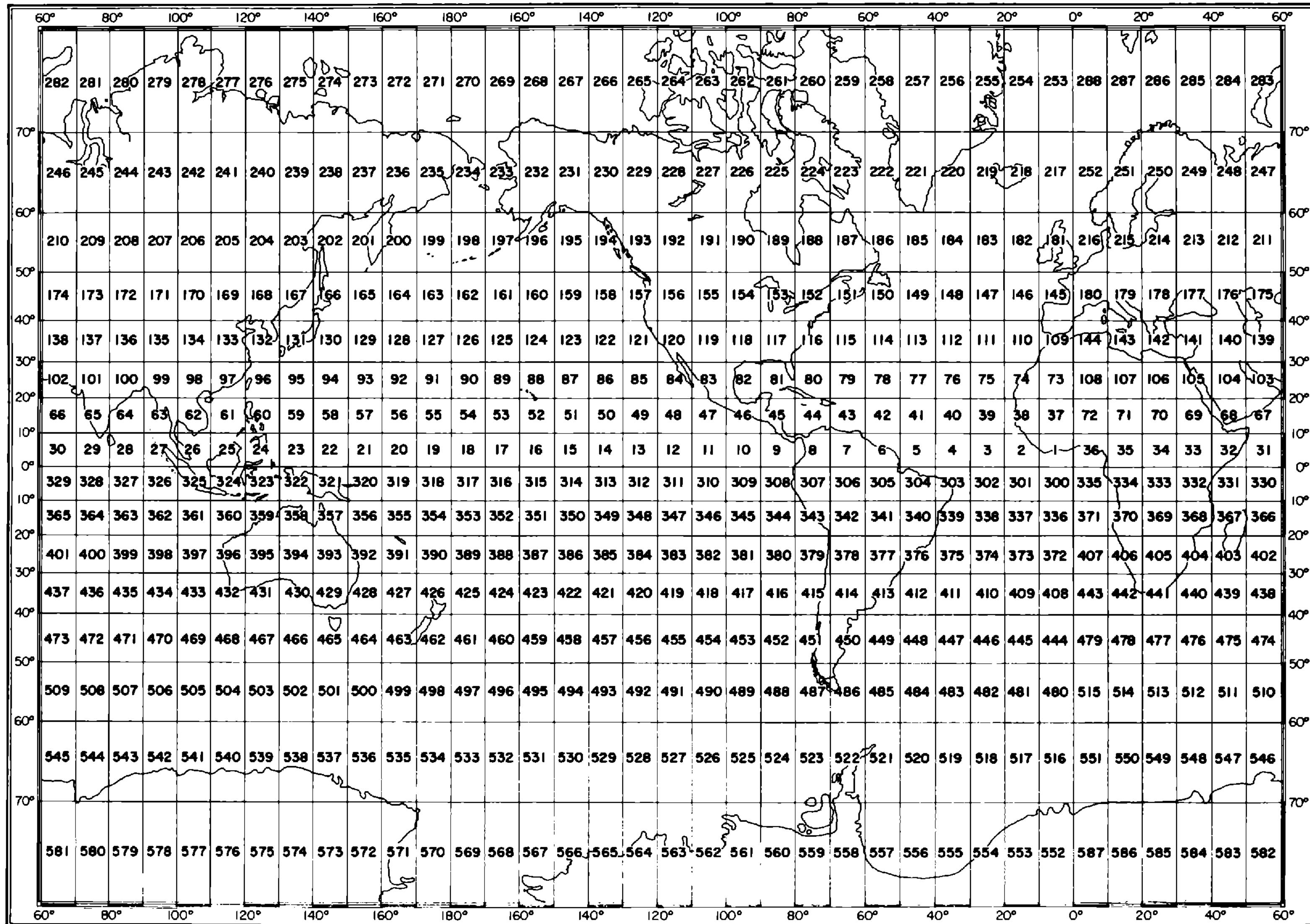
Proceedings of the Conference on PRIMARY PRODUCTIVITY MEASUREMENT, Marine and Freshwater

held at
University of Hawaii
August 21 - September 6, 1961

Edited by
Maxwell S. Doty

University of Hawaii
Honolulu, Hawaii

WORLD OUTLINE CHART
SHOWING MARSDEN STATISTICAL RECTANGLES



The papers published here were presented at a symposium held at the University of Hawaii, Honolulu, Hawaii, U. S. A., 21 August to 6 September, 1961. This symposium was sponsored by the National Academy of Sciences, the Bernice Pauahi Bishop Museum and the University of Hawaii as part of the 10th Pacific Science Congress and financially supported by Contract AT-(04-3)-15 between the Botany Department of the University and the U. S. Atomic Energy Commission.

FOREWORD AND PREFACE

The 10th Pacific Science Congress provided an opportunity to draw together the workers and work of the first ten years of augmented activity in the field of marine primary productivity. Various divisions of this Congress included meetings where productivity-related research or review papers were presented. The present publication is the result of one such effort, a symposium sponsored jointly by the U. S. Atomic Energy Commission and the Division of Botany of the Congress. This international activity involved the participation of representatives from Australia, Canada, England (Uganda), France (New Caledonia), Japan, New Zealand, the USA and the USSR, including nearly all of those who have been publishing the results of primary productivity studies made in the Pacific recently. Their names appear in the table of contents and repeatedly throughout the text.

Primary productivity, insofar as it is marine, is predominantly an activity of the benthic or the phytoplankton algae. Ordinarily, primary productivity involves the measurement of the rate inorganic materials are converted into organic materials. This measurement is made by utilizing the radioactive isotope, carbon-fourteen as a quantitative tracer. Theoretically primary productivity measurements using other elements are possible and are very much to be desired, but thus far practical means of making them have not been applied to any significant extent. At present, insofar as I am aware, direct measurement of the productivity of natural populations in terms of energy has not been attempted.

As originally planned this symposium, the papers from which are presented here, was to cover the development of the different aspects of primary marine productivity and give its current status up to August, 1961. Thus this published text should provide the reader with a source-book on primary marine productivity measurement. Since participation was wanted from as many of the individuals working on productivity in the Pacific as possible and the subject matter could not be divided equally, and for the reason that a very diverse set of individuals was concerned, only an approach to this goal has been made. I, therefore, want to refer the reader to four publications (Strickland, 1958b, 1960; Strickland & Parsons, 1960, and Vinberg, 1960) which will help to fill in the gaps the student of productivity will find in this present symposium volume.

For the reason that fresh water productivity measurement utilizing radioisotopes is so similar, a paper on the measurement of plankton productivity in fresh water has been included; though it was not presented at the symposium, itself. Similarly a criticism of chlorophyll-*a* measurement is included. To have in one place a bibliography containing most of the important papers in primary productivity up to 1960 and because the bibliographies of the individual papers were so often long and repetitive, all the bibliographic materials have been collected in one final chapter. To this bibliography have been added a number of significant papers of importance to the primary productivity worker though they were not cited in the individual texts. In corresponding with his colleagues the editor found his colleagues would like to have readily available a map of the so-called Marsden statistical rectangles extending to the Antarctic continent. Thus, as a frontispiece, one has been prepared and included.

Light has been omitted as a separate subject. A completely separate extensive symposium was organized and presented on light under the direction of Drs. John Tyler and George Clarke. This is only to emphasize the importance of light in relation to primary productivity. Currently its study is receiving a great amount of attention, and the interpretation of its effects is in a great state of turmoil.

Secondary productivity and mineralization could hardly be included in satisfactory detail for there has as yet been very little study in these areas insofar as the making of productivity-type, i.e. rate, measurements is concerned. Indeed very little information seems to be available even at the taxonomic level concerning the mineralizing rates or the mineralizing organisms themselves, but then the same statement can be applied to our knowledge of the principal primary producers, the phytoplankton species.

Two ancillary projects were undertaken to aid those contributing to this symposium. One was the compilation of as much of the phytoplankton productivity data as possible, and this (Doty & Capurro, 1961) has been published in somewhat scrambled, uncorrected form a little late for the use of everyone before the Congress. However the data were distributed several months before the Congress to the three individuals who undertook the job of producing résumés of it for the Pacific. The other project was the translation of the detailed book on aquatic productivity written by Vinberg (1960), a project that at the time of the Congress had gotten to the rough draft stage, but which has since been completed. Vinberg's publication quite naturally emphasizes the Russian and fresh-water aspects of productivity. It is thought that the information in the present publication along with that in these others will give the reader the status of primary productivity measurement on a world-wide basis as of about 1960.

The special appreciation of the editor and of the authors of the various parts of this publication must be expressed to Dr. I. E. Wallen (Marine Biologist, Environmental Sciences Branch of the U. S. Atomic Energy Commission), Mrs. Lenore Smith (Pacific Science Board, U. S. National Academy of Sciences—National Research Council) and Mr. Jan Newhouse (Dole Pineapple Company) as people who have played a great part respectively in encouraging all phases of this project, putting on, and editorially preparing and distributing the results of this symposium. These three individuals have been invaluable to the present project, but assisted the project from such positions that their assistance might not be acknowledged. The many others who gave invaluable assistance to the project include the officials of the Pacific Science Association and its biological divisions and the members of my own research staff. To name all those others whose assistance should be credited individually is an impossible task.

Maxwell S. Doty

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A SUMMARY OF PRODUCTIVITY MEASUREMENT IN THE SOUTHWESTERN PACIFIC OCEAN

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INTRODUCTION

Primary productivity studies in the western and southwestern Pacific began in 1952 with the work of Steemann-Nielsen. Later, in 1954, Dr. M. S. Doty started a program of research at the University of Hawaii with the use of U. S. Bureau of Commercial Fisheries (BCF, but then POFI) ships. Since then, two other groups have worked quite a bit in the southwestern part of the Pacific: the marine laboratory of the CSIRO in Cronulla, Sydney, Australia, and the marine laboratory of the IFO in Noumea, New Caledonia. Finally, the U.S.S.R., and very recently, the Philippine Bureau of Fisheries have started series of studies, the latter mainly in the coastal waters near Manila.

The following paper is a quick résumé of what has been done in the western and southwestern Pacific by these research groups through 1960. This covers a very large area indeed, from 30° North Latitude southward and from 125° West to 100° East Longitude. (The data themselves have been assembled and published [Doty and Capurro, 1961] in one place and thus they are not included here. Since the data for the Pacific in that volume are arranged by Marsden statistical rectangle, a frontispiece was included in this publication to show the squares in the Pacific which provided data for this paper and the other papers.)

However, it seems to me that application of the name "Pacific" should stop at the natural border which is the Philippine Archipelago in the west. Consequently, I will talk first about results in the Pacific to the east of 120° East Longitude in this sense; secondly, about the results obtained to the west of this same Longitude.

THE PACIFIC TO 120° EAST LONGITUDE

We are not aiming here at discussing all the numerous results obtained, nor with analyzing them; as a matter of fact I believe this is the work of every scientist interested in Pacific productivity.

On the contrary, it has seemed useful not to get beyond the simple stage of presenting the following three aspects of the results: where the studies have been made (density of observation), how they have been made (methods or techniques used) and what are the general results that come from them (a quick résumé of the general results).

For this reason and because of the very wide area being covered, it has seemed better not to follow the tracks of the individual ship cruises, but rather to get a general view from a geographical unitization applicable without restriction to any particular oceanic surface. For this purpose I have chosen five degree squares, that is to say, 300-mile squares. Inside each of these squares, I have put together all the results available without distinguishing the organizations from which they came (Hawaii, Australia, New Caledonia or Philippines). The Russian

data arrived too late to be incorporated but they are all from the western part of the Pacific, including the area just north of New Guinea.

I must explain the meaning of a few words or terms I am going to use. A station is one position sampled at sea during a ship cruise. The results from the special experiments conducted on the cruises are not considered. The carbon-14 results are the mean values of all the data from all the stations included in the 5 degree square. Of course, the results from the different depths are treated separately. The chlorophyll-a results are also the mean values of all the data from all the stations included in the 5° square. All the pigment values used were computed from spectrophotometric measurements by the Richards and Thompson technique (1952) or Creitz and Richards (1955) modification. Only chlorophyll-a is mentioned here and not the results concerning the other planktonic pigments: chlorophyll-b and -c and the two groups of carotenoids.

1 – Density of observations

Figure 1 shows the number of stations inside each of the 5° squares in the area with which we are dealing.

Primary productivity studies have mainly concerned two areas; first, to the east and the north of Australia to the Longitude of New Zealand; second, an area southeast of Hawaii from 10° north to 20° south and from 170° to 125° west. A few data were recently obtained along 10° to 15° North Latitude between Hawaii and the Philippines.

However, two areas are still without any observations – one at the north of New Guinea (except for the recent data obtained by the Soviet scientists, as mentioned above) and the Solomon Islands, the other to the south of Tahiti. It is particularly annoying not to have a well known band along the equator from south of Hawaii through Indonesia.

Moreover, a few areas have had many observations:

1. Close to Honolulu there are 310 stations but the greatest number of them are in inshore waters and the results are, thus, hardly comparable to those of the other geographical units.

2. Close to Manila there are 159 stations but the same criticism as above is to be made of them.

3. From the Solomon Islands to New Caledonia there are a good number of observations in the Coral Sea, in offshore waters, made by two different laboratories – one from New Caledonia, the other from Australia. From our point of view in this résumé, this southwestern part of the Pacific is probably the one best known.

4. Close to Sydney there are 64 stations; a few of them still are in the neritic area where the Port of Sydney and the coast could have had an influence. However, a good number are out of this area and the mean values can be used in deriving an understanding of the general phenomena of the Pacific Ocean.

Methods of observation

Some of the numbers of Figure 1 are underlined to show that, at these stations, the routine measurements were made at the four depths of 0, 25, 50 and 100 meters. The underlined numbers are all confined to the seas around New Caledonia and east of Australia. When there is no line under the number, only the surface was routinely measured; some other depths have also been studied but not regularly and no comparison can be made. Two techniques of measuring the productivity of water samples using carbon-14 are used in the southwestern Pacific: the Hawaiian method where only surface samples were used and the Australian method with samples from the four depths.

The French laboratory in New Caledonia at first used both of these methods but finally came to use routinely the Australian method. This choice explains the localization of the so-called 4-depth stations. Without stating that one method is better than the other, it is certain that a difference in technique can cause a difference in the results. This very important problem of the value of the results is discussed in succeeding papers in this volume. For now, one could say that comparison between the methods seems possible but only after a very precise study will we be able to accept either a direct comparison or a comparison after applying a

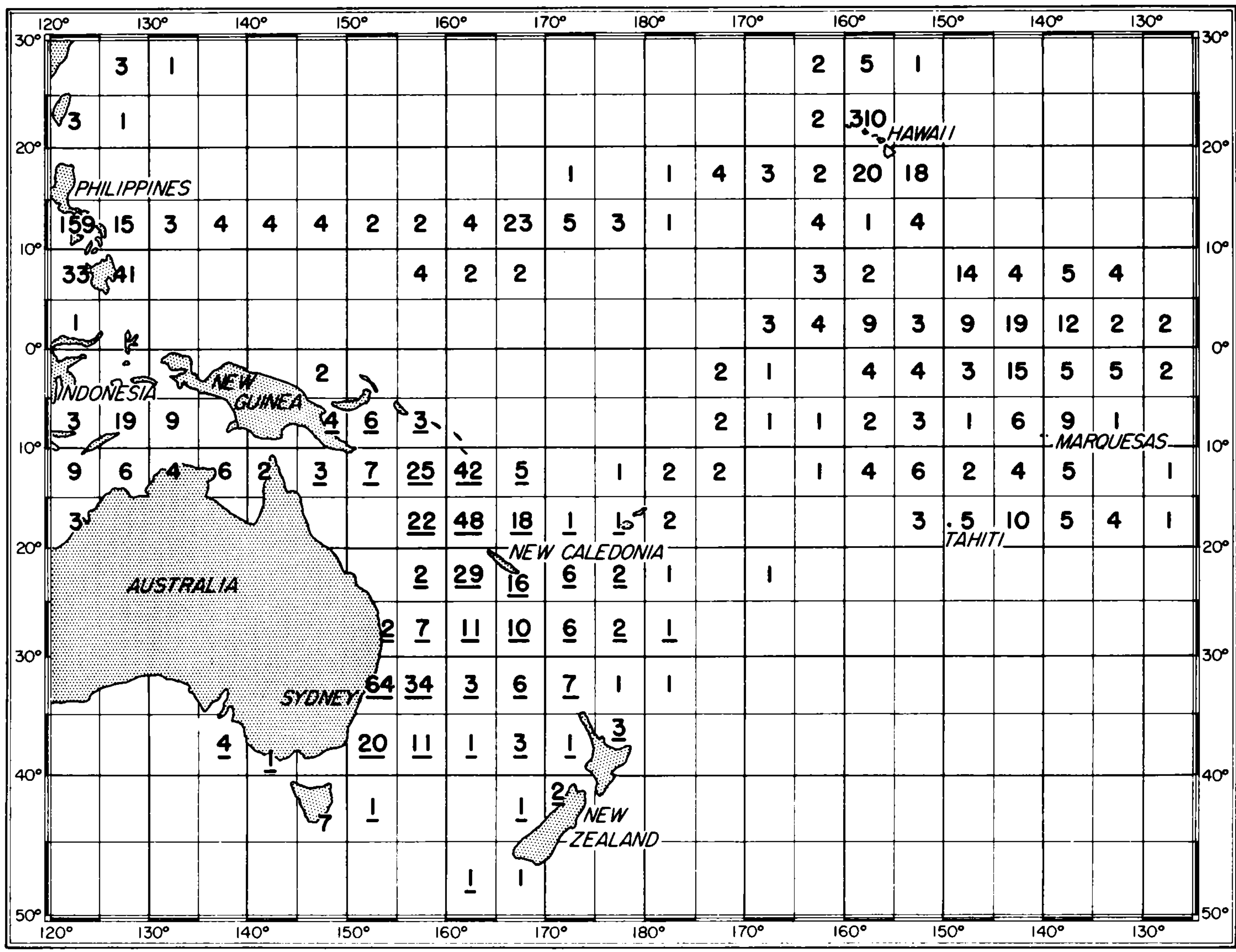

Figure 1—Distribution of the number of stations in the southwestern and western Pacific area. The underlined numbers are the so-called 4-depth stations.

factor which is yet to be defined. In any case, it seems quite desirable to standardize the method in this area of the Pacific.

Quick résumé of the results

Although the total number of observations is already significant, it is obvious that these results, being from such a large area, are too few and surely not definitive; even for the best known areas – so, what we say now can only be said to be tentative.

Moreover, after considering the more apparent phenomena, I will insist on a few remarks which seem to me very important for the near future if we desire to reach as soon as possible the best possible understanding of the general aspects of primary production in the Pacific. This is, I believe, the main idea of the symposium papers which follow.

Fixation of the carbon

The surface observations are the only ones numerous enough to be used in the study of the southwestern Pacific as a whole. Figure 2 shows the geographical distribution of the mean values in the 5° square units.

South of Hawaii, between 10° and 5° south, there is a strip of water where the primary productivity values are relatively high in comparison to the values for adjacent waters. This fact is surely related to the localization of upwelling in a zone along the equator which has been shown by the U. S. Bureau of Commercial Fisheries (BCF) hydrological studies. The fixation rate for carbon is very low from the Marquesas Islands to Tahiti, in spite of the numerous islands of the Tuamotu Archipelago. These peaks with atolls on their tops are not the sites of any special degree of phytoplankton growth. This is to be associated with the relative stability of the surface hydrological conditions that the BCF studies have demonstrated for this area.

The few results obtained between Hawaii and the Philippines from the latitudes 10° to 15° north seem to show a continuous trend of the primary productivity characteristics if they are compared with those south of Hawaii. We must conclude that the high rate measured between 170° and 180° east is only so because of local studies made in inshore waters of the Marshall Islands. Elsewhere, the samples are from offshore waters and show that the rate is low between 15° and 10° north but higher between 10° and 5° north.

Along the Solomon barrier which continues on to New Guinea and the New Hebrides, there is relatively high productivity. It is quite unfortunate that we do not have any information from east of this area, for we cannot follow the evolution of the water masses across the Pacific. However, the high values of the rate of fixation are localized where the hydrological studies show that eddies exist; the IFO studies have already brought these results to light. So, there is a very big difference in the growth of oceanic phytoplanktonic populations between: first, the Tuamotu area where the atoll-topped peaks seem not to cause any better growth and, secondly, the Solomon Archipelago where the barrier seems to cause the initiation of some hydrological systems around which are organized some productive areas.

South of the Solomon Islands, the Coral Sea is low in productivity, but the Tasman Sea further south has a rate of fixation that begins to be higher, and especially is higher from 25° south. The very southern part of the Pacific is generally much more productive than the tropical water masses and often more productive even than the equatorial area. This is obvious around New Zealand.

Finally, to the north of Australia, in the Arafura, Timor and Banda Seas, there is high productivity which could be related to the relative proximity of land.

Concentrations of chlorophyll-a

Just a few areas in the southwestern and western Pacific have been studied for the concentration of planktonic pigments, mainly chlorophyll-a. This is quite evident when you look at Figure 3 where the mean values are shown by 5° square units. The results are expressed as mean values in milligrams per cubic meter (mg/m^3) of chlorophyll-a. The results are too few to draw general conclusions. However, we can point out a few things for some areas.

South of Hawaii, the values are higher between 5° north and 5° south than in the waters situ-

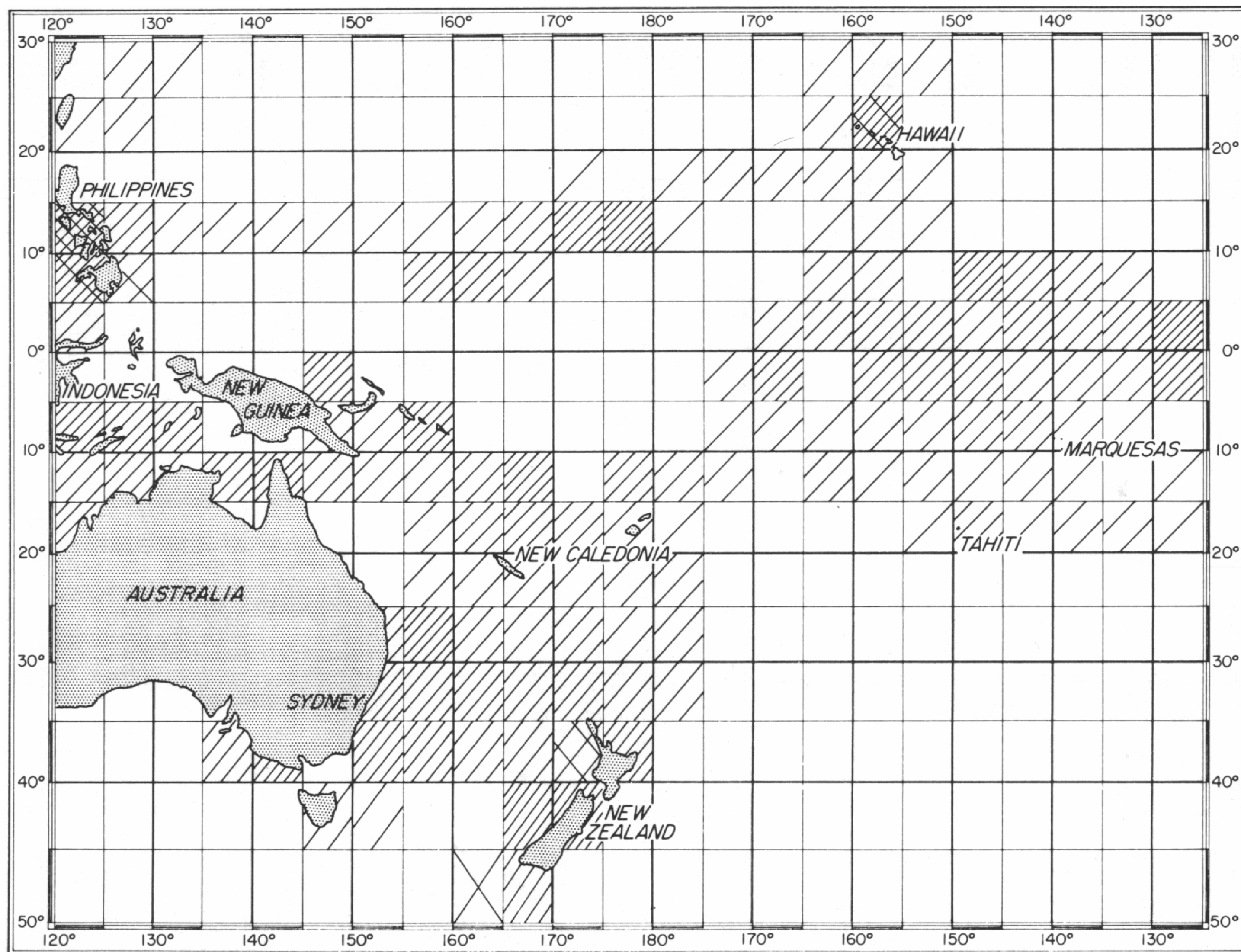

Figure 2—Distribution of the rate of fixation of carbon-14 in the surface samples. One line from upper right to lower left–0.1 mg $C/h/m^3$; Two lines from upper right to lower left–0.2 mg $C/h/m^3$, etc; One line from upper left to lower right–1.0 mg $C/h/m^3$, etc.

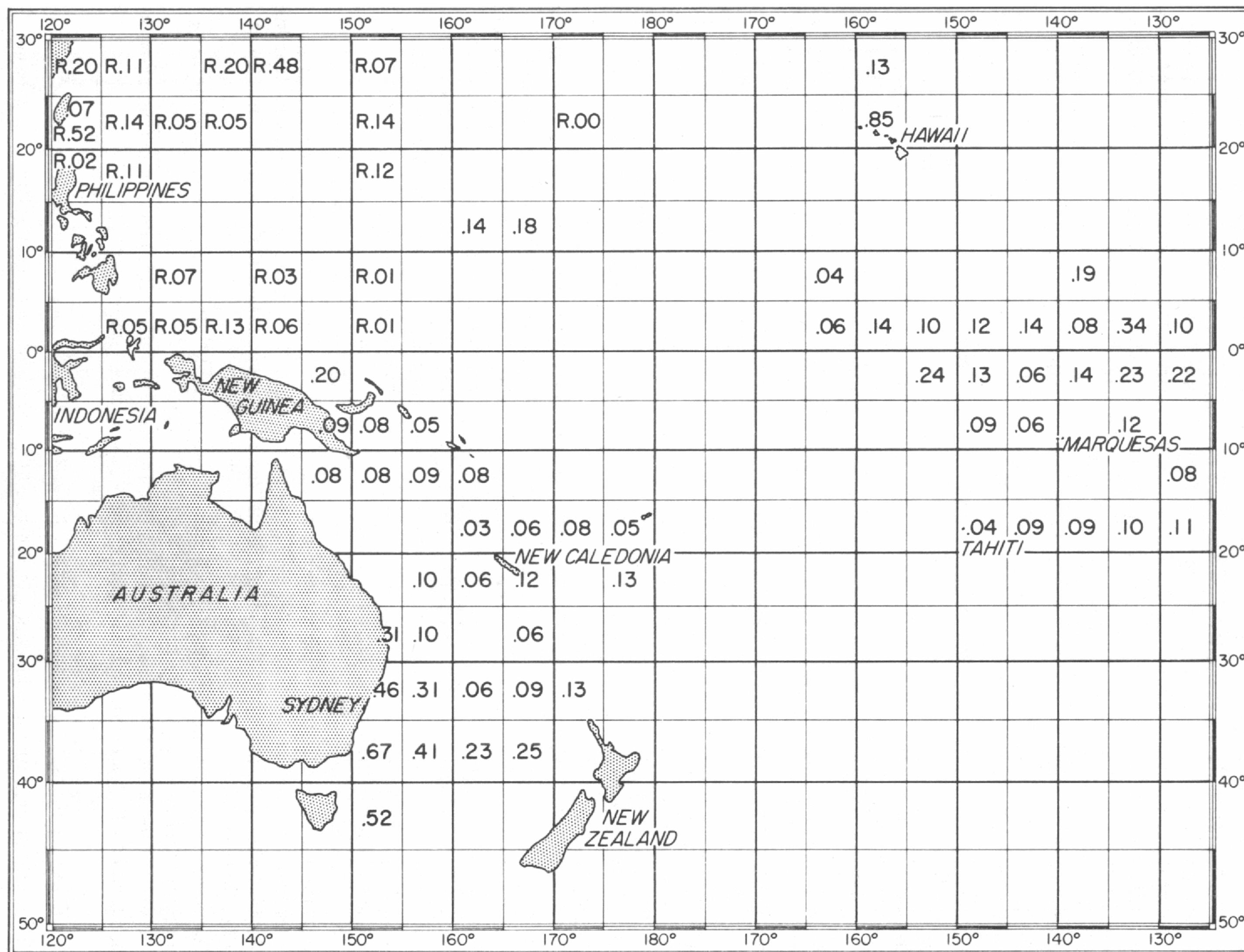

Figure 3—Distribution of the concentrations of chlorophyll-a (in mg/m^3) in surface samples. Values preceded by an "R" are Russian data for fixation of carbon-14 in surface samples (mg C/h/m^3).

ated further south. This chlorophyll-a rich strip of water is almost at the same location as the productive water discussed above.

North and east of Australia, the only area in the southwestern Pacific where routine observations have been made, the values are high near the Australian shore and in the southern waters south from 35° South Latitude. The Coral Sea, on the contrary, has low concentrations of chlorophyll-a. As a matter of fact, we notice here about the same values as observed at the same latitude around Tahiti.

Elsewhere, the only noticeable phenomenon is the lack of observations. It would be very useful to multiply the collections, mainly between the already known eastern and western areas and especially along the equator, between 5° north and 10° south. The results could fill some of the gaps in our knowledge of what is going on in the western Pacific.

It is fair to say that the collection of an adequate number of planktonic pigment measurements is slowed by some of the practical aspects of the method. During this symposium the techniques will be discussed and there must be no doubt that suggestions for improvement and standardization of this technique will be welcomed.

Other results

Besides the studies mentioned here, it is hoped that measurement of nitrate concentrations and light will become routine. Some have already been made by the different staffs in Hawaii, Australia, New Caledonia and on board the Soviet research ships, but they are too few to be noticed here. However, I think that the measurement of light penetration is one of the very important observations to make in any productivity study, and I would suggest this be done even if one is able to use only the Secchi disk.

TO THE WEST OF 120° EAST LONGITUDE

Studies of this part of the Pacific have begun only just recently and have been mainly made around Manila. The data have been worked on the same way as the others. The results appear in Figures 4 and 5.

There has never been any study of the planktonic pigments in this area. As for the rate of fixation of carbon, only the surface data have been retained although a few determinations at different depths have been made. All the measurements were made with the Hawaiian technique.

The number of stations, shown in Figure 4, is already dense enough to get a general idea of the primary production in this part of the ocean. The distribution of the rate of fixation, shown in Figure 5, shows that there are some extremely productive areas. In any case, the ability of the phytoplankton to synthetize organic matter photosynthetically is generally much higher than in the southwestern Pacific.

Two areas are especially productive – one around the Malacca peninsula and south of Vietnam; the other one in the Philippines. It could be that this comes from the proximity of land; however, the uncontested average richness of the China Sea leads one to suppose that the hydrological characteristics of this water mass are also responsible for the great activity of the phytoplankton.

The values are high in the Java Sea, south of Borneo and Celebes Islands, a marine area where high turbulences are very probable.

Finally, in the eastern part of the Indian Ocean close to Australia, one can see an area of high productivity to the north and one having very low values to the south.

General conclusion

The study of primary productivity in the southwestern and western Pacific is now being made by different staffs who have worked with their own methods and in areas that they have chosen by themselves. There has been no real mutual planning although cooperation is effective at both the technical and practical levels.

Because of the now known results and the desire which all of us have of getting a better understanding of the characteristics of the Pacific Ocean, it seems desirable now to look

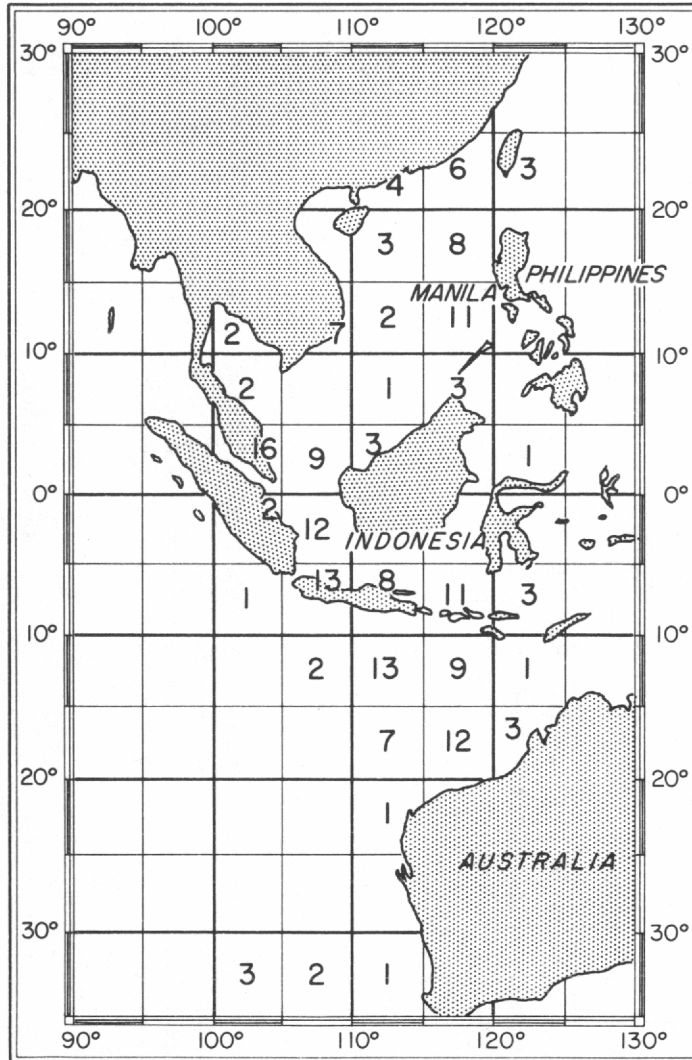

Figure 4—Distribution of the number of stations from west of 125° East Longitude.

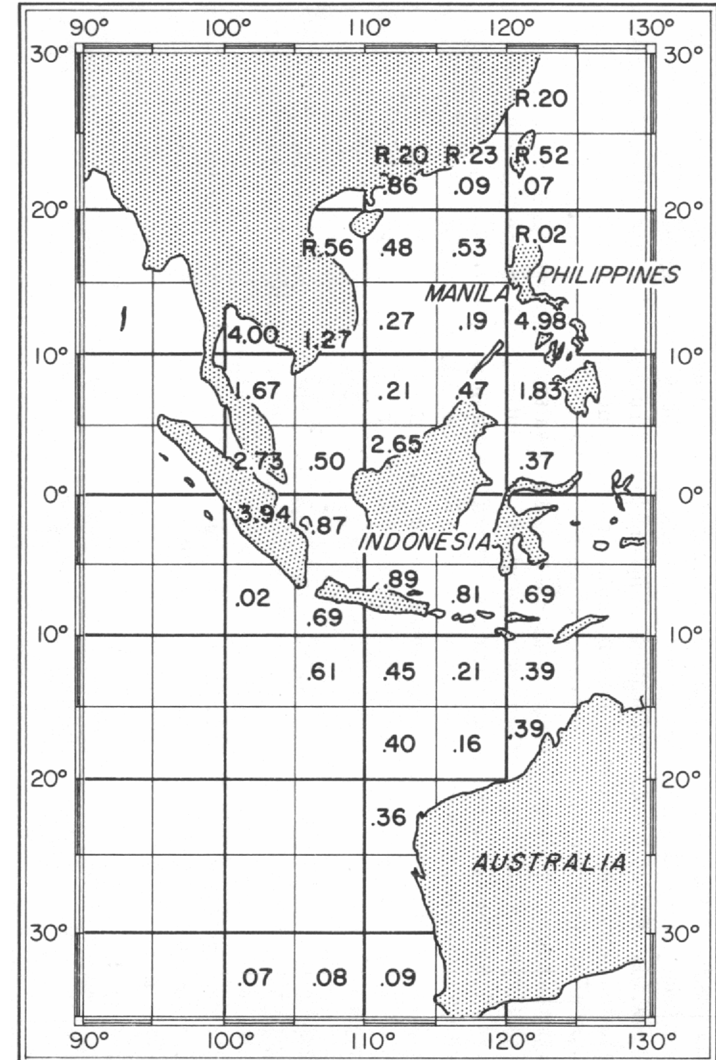

Figure 5—Distribution of the mean values for fixation of carbon-14 in the surface samples to the west of 125° East Longitude.

toward unification, or standardization, of the means of obtaining data and the programing of research.

About the methods, three principal techniques, including the Soviet one, of using carbon-14 in measuring primary productivity are in use; we ought to define very soon how we can compare data from these three and what are the best conditions for their use. The measurement of pigments has to be generalized and it is hoped that some of the not very clear results which are sometimes obtained can be explained. The measurement of light penetration should be extended as much as possible as a routine part of scientific cruises. Finally, we hope that the physical oceanographers will become more interested in studying the concentration of phosphates and nitrates in the water.

It is now hoped that, besides the areas which have been studied already, more attention will be paid to studies of the equatorial area, especially the relatively unknown equatorial areas between 175° west and 125° east. For this area there is a lack of observations which is depressing when one tries to get a general idea of the productivity of the Pacific.

Finally, one can emphasize the very special aspect of the China Sea in respect to the rate of carbon fixation. This alone is enough to make desirable a more complete study of this area.

A SUMMARY OF PRODUCTIVITY MEASUREMENTS IN THE NORTH PACIFIC OCEAN

O. J. KOBLENTZ-MISHKE
Institute of Oceanology
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The purpose of this report is to review the research on primary production and plant pigments made in the North Pacific (Fig. 1).

Sources of Information

We have data at our disposal, both published and unpublished, gathered by American, Japanese, Canadian and Russian expeditions from 378 stations, but, unfortunately, some data are lacking. The results obtained during "Transpac" in 1953 near the Aleutian Islands are only available in summarized form, and but 16 out of 38 stations are presented in the published material on the cruise of "Riuofu Maru" in the summer of 1958. The paper by Miyake which deals with the determination of primary production and chlorophyll in the inshore waters of Japan and the data gathered in the inshore waters of Canada have not been available. Also, we have no data on nutrients and light.

The contribution of each country to the research on primary production in the North Pacific Ocean has been as follows: the U. S. A. from 1953 – 1960 carried out measurements of primary production by means of carbon-14 technique and plant pigments at 113 stations during 3 cruises; the U. S. S. R. from 1954 – 1959 carried out measurements of the primary production by means of carbon-14 and O_2 methods at 105 stations during 7 cruises; Japan on 4 cruises from 1957 – 1960 made determinations of production by the carbon-14 method and chlorophyll at 138 stations; and Canada has carried out regular observations of primary production and plant pigments at station "P" from the weather-ship since 1959. Most of these data concern surface productivity with only a small amount of data shown for production in the full water column.

The general information on the measurement of primary production and plant pigments in the Northern Pacific is given in Table 1 and Figures 1 & 2. It is obvious that the majority of the measurements were determined in the region of Japan and between 160° and 178° W. The Japan, Bering, and especially the Okhotsk, Seas were studied only occasionally and but few measurements were made in the Alaska Bay.

Table 1 and Figures 1 & 2 give only the general picture, since evaluation of the yearly production would require data concerning the different types of water in all seasons. Therefore, even an estimation of complete productivity on the basis of available material requires subdivision by seasons and also division of the North Pacific into districts which differ in productivity. For the areal division, the charts of water masses compiled by Dobrovolsky, Fleming and Uda were used. These charts were plotted on the same blank-map and the boundaries of the masses were drawn on the chart (Fig. 3). Since the biogeographical boundaries are usually the same as the hydrological boundaries, these boundaries were used in the cases where the classification of data could not be accomplished in other ways. For example, the parallel taxonomic investigation made during the cruises of the "Vityaz" permitted the biogeographical classification of the material.

Table 2 shows the relative abundance of our knowledge for the different types of waters in different seasons. The greatest quantity of the data on primary production were obtained in the

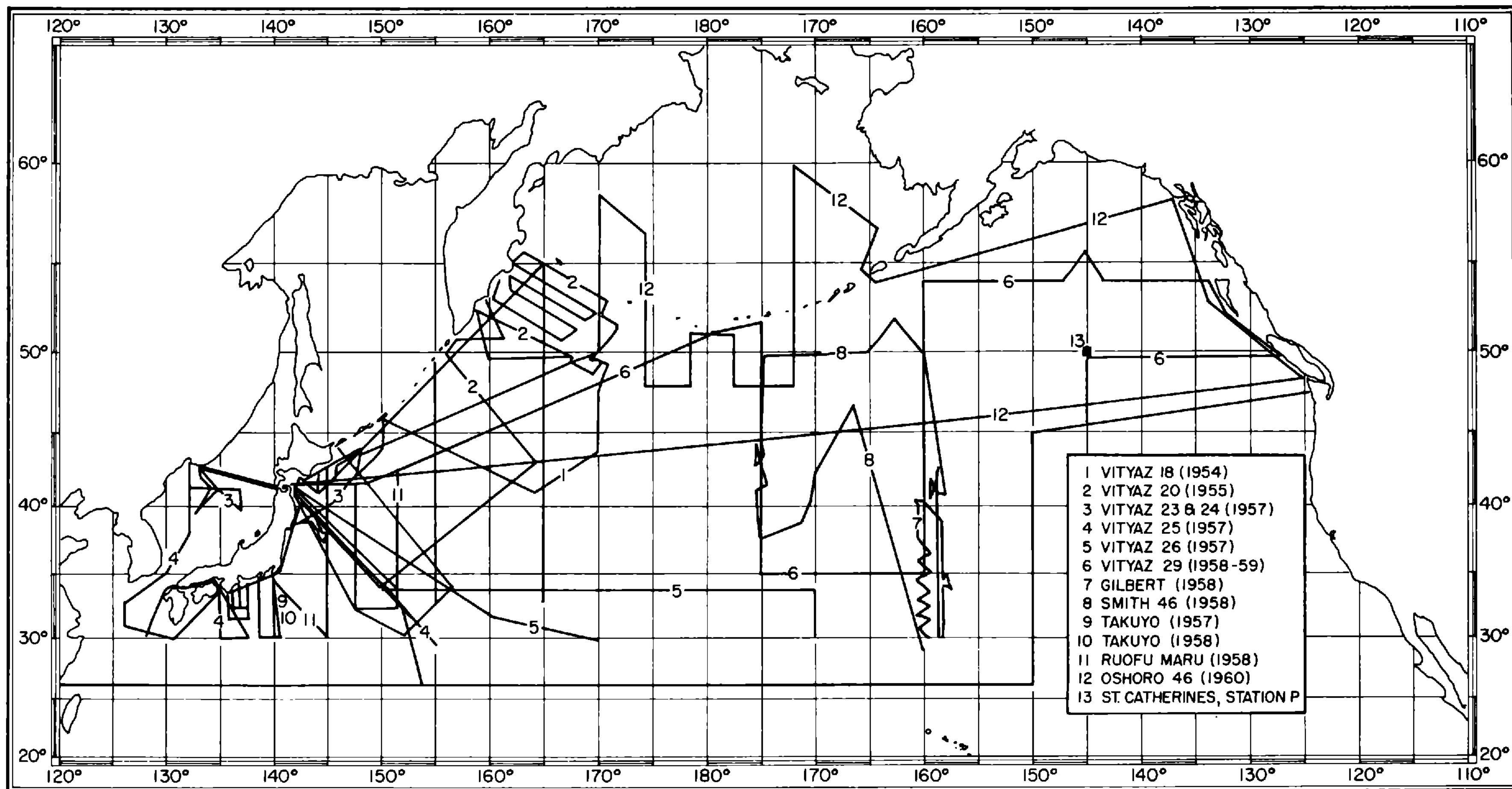

Fig. 1—Cruises on which primary production and plant pigments were examined.

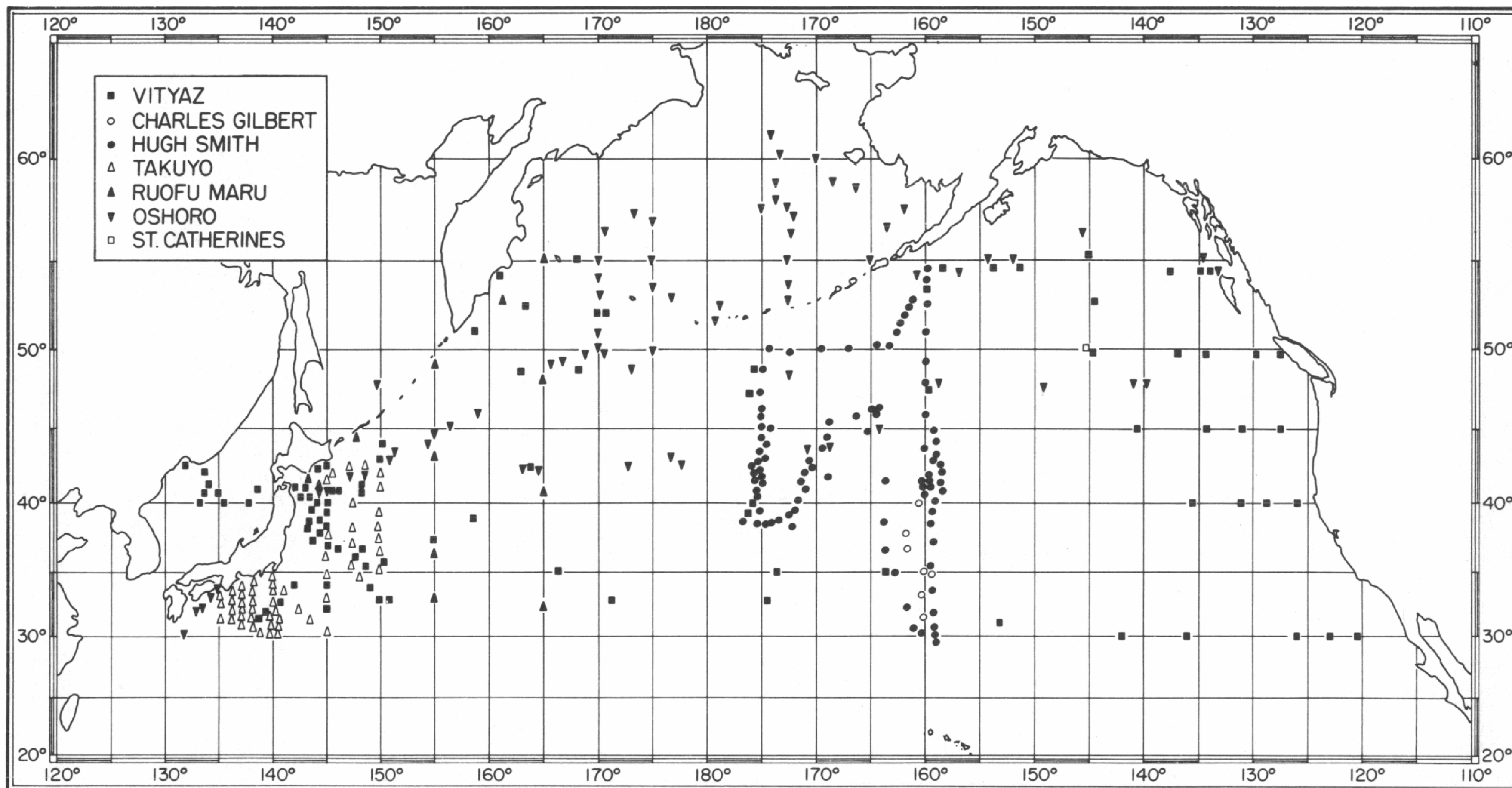

Fig. 2—Stations on which primary production and plant pigments were estimated.

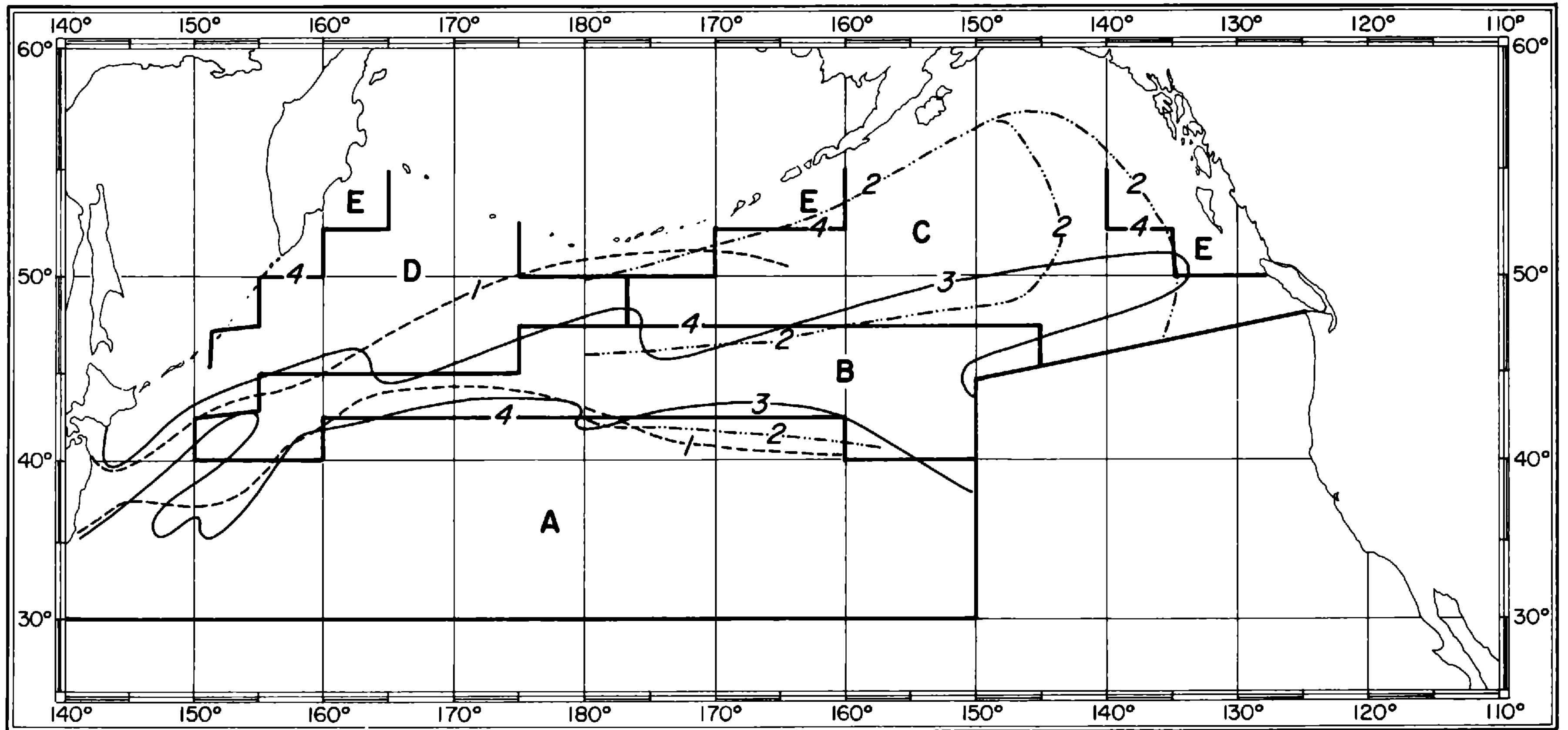

Fig. 3— Division of the North Pacific into natural districts.

Table 1 — General Information of the Investigations of Primary Production And Plant Pigments in The North Pacific

Date	Research ship and expedition	Region	Number of stations	Character of investigations	Reference
1953 VIII-IX	Transpac	Aleutian Islands	10	C-14, Chlorophyll-a	Holmes, 1957
1954 IX-X	Vityaz, 18 cruise	Northwestern Pacific	20	O_2	Bogorov & Beklemishev, 1955
XII	Charles Gilbert	160°W, 30°-40°N	7	C-14, Pigments	Unpublished*
1955 V-VI	Vityaz, 20 Cruise	Northwestern Pacific	14	O_2	Koblentz-Mishke, 1957
1957 V-VI	Vityaz, 23 & 24 cruises	Japanese Sea & adjoining part of the Pacific	28	C-14, O_2	Sorokin & Koblentz-Mishke, 1958
VII	Vityaz, 25 cruise	Standard Section	10	C-14, O_2	Koblentz-Mishke, in print
VIII	Takuyo	Southward of Japan	19	C-14, Chlorophyll-a	Saijo & Ichimura 1959, 1960
XI	Vityaz, 26 cruise	Standard Section	3	C-14	Unpublished*
1958 V	Takuyo	Southward of Japan	18	C-14, Chlorophyll-a	Saijo & Ichimura 1959, 1960
VII-IX	Ruofu Maru	Northwestern Pacific	38	C-14, Chlorophyll-a	Ichimura & Saijo 1960
VI-VII	Oshoro, 45 cruise	Southward of Japan	8	C-14	Unpublished*
VI-VIII	Hugh Smith	Between 150° and 180°N, from 30°N to Aleutian Islands	99	C-14, Pigments	Unpublished*
X-XII	Vityaz, 29 cruise	Northeastern Pacific	22	C-14	Koblentz-Mishke, in print
1959 III	Vityaz, 29 cruise	Standard Section	8	C-14	Unpublished*
VII-VIII	St. Catarines	Station "P"	7	C-14, Pigments	McAllister, Parsons, & Strickland, 1960
1960 VI-VIII	Oshoro, 46 cruise	Bering Sea North Pacific	68	C-14	Unpublished*

*Since the time this manuscript was prepared, these data have been published (Doty & Cappuro, 1961), at least for the most part. Ed.

summer in the transition zone and in the subtropic waters (for which division into seasons was unnecessary). The subarctic water masses were relatively well studied in the summer. The poorest material in our possession concerns the inshore waters, although this could be supplemented by the Japanese and Canadian results. From the seasonal point of view it will be noted that the main gaps are in the autumn-winter period.

Because of the absence of much important information, only the spring-summer period can be used for a comparison of the mean production obtained in waters of different types. At this period of the year, the surface primary production was as follows: in the transition zone, 5 mg C per m^3 per day; in the western subarctic water mass, 10; in the eastern subarctic water mass, 3; and in inshore waters about 50. The mean value for the subtropic water mass was 1.2 the year round.

Far fewer data are available for plant pigments than for primary production. Chlorophyll-a was the most investigated of all plant pigments, and the investigations were made in the summer.

Table 2 — The Number and General Character of Data Gathered in Different Waters

Types of waters and seasons		Primary production (mg C per cu.m per day) Number of measurements	Mean value	Limits of deviations	Chlorophyll-a (mg per cu.m) Number of measurements	Mean value	Limits of deviations
Subtropical water mass		48	1.3	0.1–10.3	14	0.79	0.06–1.73
Transition zone	winter	1	0.4				
	spring	5	3.6	0.7–6.2			
	summer	87	7.4	0.8–28.5	94	0.77	0.04–3.60
	autumn	7	4.8	0.3–9.2	15	0.93	0.333–1.65
West subarctic water mass	winter, spring, summer, autumn	26	9.7	1.8–54.9	7	0.23	0.10–0.78
East subarctic water mass	winter	8	2.1	0.3–4.0			
	spring						
	summer	330	3.1	1.5–28.2	20	0.61	0.27–3.01
	autumn	10	3.1	0.3–10.0			
Inshore (neritic) zone	winter	2	0.9	0.4 & 1.4			
	spring	11	106.0	6.0–530.0			
	summer	14	19.5				
	autumn						

In the surface of subtropic, transition and subarctic waters the mean amount of chlorophyll-a varied very little, being in boundaries of 0.6–0.8 mg per m^3. In the neritic zone the mean amount was 1.3 mg per m^3 on the average.

Reliability of Data

In general, the material on production and especially on plant pigments is not statistically representative. The two reasons for this situation are the scarcity and unevenness of the material. The unevenness of the material in turn is caused by irregularities in the primary production measured and also by differences in the methods used by the investigators. Every method has both systematic and accidental deviations. It is difficult to say anything about the systematic errors in the work of the American and Japanese investigators. Unfortunately, it must be noted that our data are too low. A systematic error of 20–30% occurs because of the inaccurate determination of the stock activity. This error is made not only in our measurements but also in those where, as in our case, window-counters were used. This error occurs because the effect of radiation scattering in the layer of $BaCO_3$ is disregarded. Another source of the discrepancy between our data and data of foreign investigators lies in the different conditions of illumination. Our measurements were carried out in daylight, therefore the photosynthesis in the tropics was depressed by excessive illumination. On the other hand, photosynthesis was depressed in boreal waters by use of the "tank" method with superabundant light.

The following method was employed for determining the accidental deviations. The results of three cruises: the 29th of "Vityaz," the 46th of "Hugh Smith" and the 46th of "Oshoro" were statistically analyzed. The mean production and the relative deviations were calculated for each separate station. All the mean data of the production were classified and for every group a standard deviation was calculated. The calculation involved the use of all deviations found in the data belonging to each separate group. The results are summarized in Fig. 4. It should be noted that accidental deviations occurred not only because of errors in the method used, but also because of the patchiness of plankton.

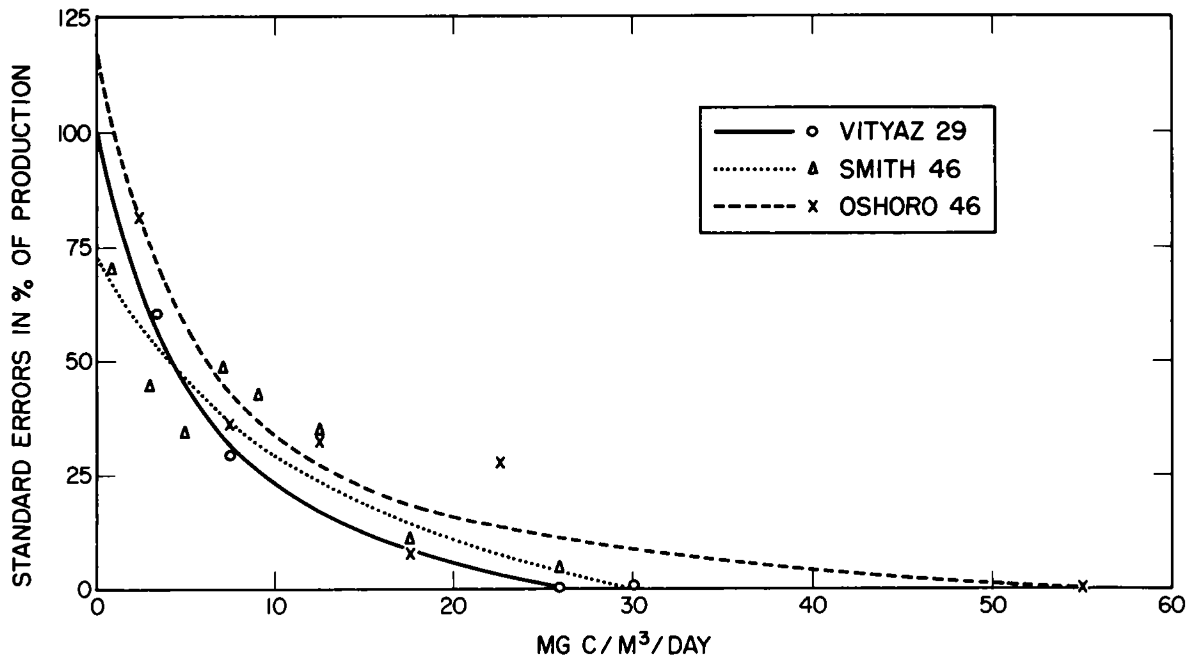

Fig. 4—Standard deviations of the mean values obtained for the data of Vityaz 29, Smith 46, and Oshoro 46.

Everything said thus far concerns only production at the surface. There is not enough data for the evaluation of the mean column production since use of the results obtained in "tank" experiments for the calculation of production in the whole water column seems not to be sufficiently reliable. It seems much more reasonable to use the relation between the production in the whole water column and that on the surface, obtained "in situ." Table 3 presents all such coefficients at our disposal, and these, it will be noted, are not numerous. Most of them differ in the limits of 14–26 with the exception of those for the transition zone in the spring where they are higher (40–60).

Table 3—Relationships Between Primary Production in the Water Column and that on the Surface, Obtained by Different Authors

Character of waters	Seasons	Ratio of production in water column to the production on sea surface
Mixed zone	spring	44, 58
	summer	24, 26, 24, 14
	autumn	24
Subarctic water mass	summer	40, 20, 25, 39, 13, 17
	autumn–winter	21, 26, 26, 19, 14

Summary

1. The study of the primary production of the North Pacific was begun in 1953 during expedition "Transpac." In 1953–1960 measurements of primary production and plant pigments, especially chlorophyll, were made at about 400 stations. The most abundant material was collected near Japan and between 160° and 178° W; the poorest coverage was in the seas of the Far East and in Alaska Bay.

2. Classification of the data was made by seasons and by types of waters. It was found that the most abundant material on both primary production and pigments was collected in the tran-

sition zone in the summer, the poorest in the inshore waters for all seasons, and in the remaining regions in the winter and autumn. The subtropic and subarctic waters in the spring-summer period were moderately well studied.

3. The highest production was found in spring and summer in the neritic zone. The next highest production was found in the subarctic and transition waters, and the least, in the subtropical waters.

4. When comparing the material, the accidental deviations were analyzed for measurements of primary production made during the 46th cruise of the "Oshoro" (Japan), the 29th cruise of the "Vityaz" (USSR) and the 46th cruise of the "Hugh Smith" (USA). It was found that in the cases of low production the largest deviations occurred in data from the "Oshoro," and the smallest in data from the "Hugh Smith." In the cases of high production, the largest deviations also belonged to data from the "Oshoro"; the smallest were found in data of the "Vityaz."

5. The relation between the production in the water column and that on the surface ranges in boreal waters from 14 to 26 and in the transition zone in the spring from 40 to 60.

A SUMMARY OF PRODUCTIVITY MEASUREMENTS IN THE SOUTHEASTERN PACIFIC OCEAN

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INTRODUCTION

For purposes of this discussion, the area included within the southeastern Pacific is bounded on the northwest by a line extending from Hawaii to the southern tip of Vancouver Island, British Columbia; on the east by the land masses of North, Central, and South America; and to the west and south by a line extending roughly southeast from the Hawaiian Islands to the Antarctic Continent but not including any portion of the Marquesas Islands area. For convenience, the area has been further subdivided into four regions: a northern and a southern region north and south of 25°N and 25°S, respectively; and northern and southern equatorial areas lying between the equator and 25°N and the equator and 25°S, respectively. Each of these four regions has been further subdivided into inshore and offshore areas, the limit being taken at 60 miles from the continents. These divisions are arbitrary. They have no inherent biological, chemical, or physical significance except that the inshore areas are often more productive than the offshore areas.

Hydrographically, this entire area includes within its boundaries portions of the California Current, the North and South Equatorial Currents, the Equatorial Counter Current, and the Peru or Humboldt Current. In addition, many regions along the North and South American coasts as well as the region between the North Equatorial and Equatorial Counter Currents are characterized by upwelling, a process which is of considerable importance and interest to workers in the field of primary production. In addition to being an area of considerable scientific interest in itself, portions of this area support a large tuna fishery and guano industry which owe their ultimate existence to primary production. Notwithstanding the commercial importance of these and other industries which are more or less directly dependent upon the fertility and productivity of the sea, our observations are woefully inadequate. As a result, our knowledge of the biology of this vast area is inadequate and still very much in the early descriptive stage. This fact is quite evident from the number of observations available, summarized in Figure 1 and Tables I-XII. Fortunately, interest in the physical, chemical, and biological processes in this section of the Pacific is increasing, and funds for research are being provided by universities, national, and international agencies.

The sources of information used in this compilation have been various. The author is greatly indebted to a number of scientists for making available to me unpublished material and for answering queries about data already in print. Dr. George Anderson of the University of Washington has provided me with a concise summary of the productivity program being carried out by the Department of Oceanography in the waters off Washington and Oregon. Unfortunately, none of the data were available for incorporation into the data summary at the time of writing. Dr. Maxwell Doty, our chairman, kindly provided me with information obtained by himself and his colleagues in the Bureau of Commercial Fisheries at Honolulu.

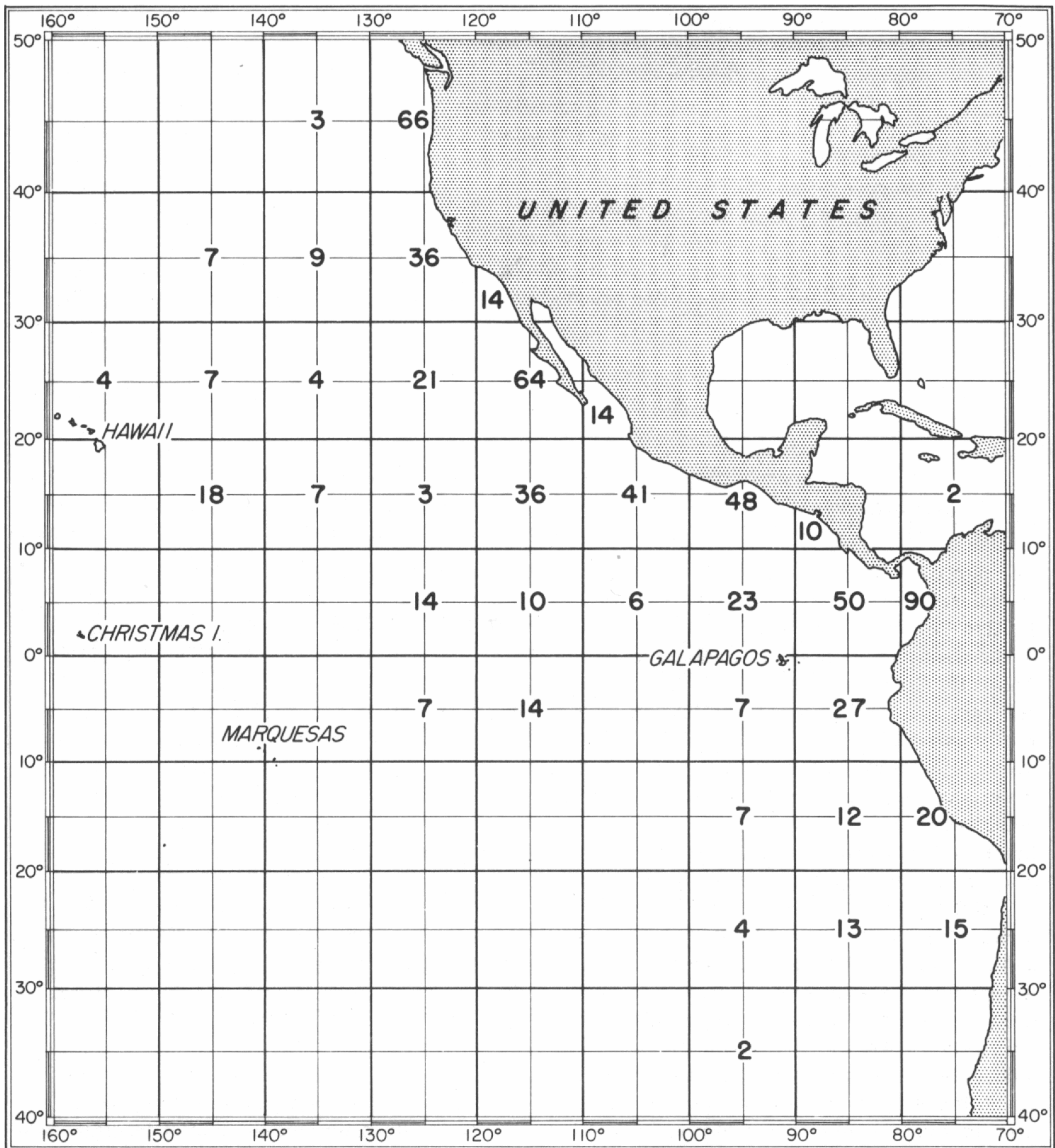

Figure 1—Distribution of the number of stations in the southeastern Pacific area.

Mr. Eric Forsbergh of the Inter-American Tropical Tuna Commission kindly allowed me to summarize the productivity data obtained by the Inter-American Tropical Tuna Commission, much of which has only appeared in Progress Reports and Cruise Data summaries. Dr. Koblentz-Mishke has answered questions about the translation and interpretation of techniques used on Cruise 29 of the Vityaz. The Vityaz data used in the summary were obtained from the World Data Center A (see also Doty and Capurro, 1961) and unfortunately appear to be somewhat incomplete. Finally, I am indebted to Mrs. Dorothy Burgess, who has painstakingly rechecked the compilations for errors and completeness. Any omission or inaccuracies, however, are the sole responsibility of the author.

All workers in the field of primary production owe a debt to Prof. E. Steemann-Nielsen (1952) who introduced the carbon-14 method of measuring primary production and without whose aid, direct and indirect, the summary would have been impossible.

OBSERVATIONAL PROGRAM SUMMARIES

In the opinion of the author, the measurement of primary productivity is not an end in itself, but provides an important if not a necessary adjunct to other biological, physical, and chemical observations. For this reason, a summary has been prepared for each cruise or expedition, listing the types of observations that have been made, including, of course, the types of productivity measurements.

We are interested in understanding as well as describing a dynamic biological regime. An isolated measurement of the rate of primary production in a given location is useful only in a descriptive manner and should be supplemented whenever possible with additional observations. In fact, it may even be argued that an isolated rate measurement is little better than a standing crop measurement, since we have little understanding of the constancy of the rate as a function of space or time.

DATA SUMMARIES

In addition to preparing a listing of primary production and other synoptic observations in the southeastern Pacific, a summary has been prepared for each region defined above which lists: a) the number and type of measurements made in the inshore and/or offshore portions of each region; and b) the lowest, median, and highest value observed in each of the categories, ignoring the date or season of the observation. In the case of the Scripps Institution of Oceanography observations made by the author, the fact that observations have been made is indicated in the observational program summaries, but the values have not been included in the data summaries (Tables A-H) because they are suspect. Except in the case of the observations made by the author and Mr. Forsbergh, the measurements are not comparable in terms of techniques and sampled depths. Thus it has been necessary to make several separate listings for the same area.

CONCLUSIONS

A perusal of the data forming the summaries in Tables A-H shows in general the rate of primary production inshore exceeds that observed offshore. A notable exception is evident in Table B (0-25°N) where the median offshore surface _in situ_ value exceeds the comparable inshore value. This exception results from a high proportion of observations being made in the region of the Costa Rica Dome (see Holmes, Schaefer, and Shimada, 1957). This offshore area is highly productive as a result of surface nutrient enrichment resulting from circulation features of the area.

In upwelling areas the rates of primary production are higher than in adjacent non-upwelling areas as expected, but such features are not readily apparent in the data summaries. The causes of variations in production rates are not understood completely and are dependent upon numerous biological, chemical, and physical processes and their interactions. These summaries tend to obscure these interrelationships, but to interpret the data further is beyond the scope of this short paper. Unfortunately, very few of the data included in this summary have been the subject of scientific papers. It is hoped that those individuals collecting the data will report upon them in the near future.

Some general comments do appear justified, and these should be taken into consideration when primary production measurements are made in the future:

1). There is a necessity for standardizing on one basic routine technique which all investigators should use. Such a technique is, of course, a minimal one and should be supplemented whenever possible by more specialized types of measurements (e.g., saturation curves, nutrient supplement studies, etc.) which are of interest to various investigators. Perhaps agreement on such a basic technique can be reached at this meeting and given a trial during the forthcoming International Indian Ocean Expedition.

2. Both seasonal and geographic coverage is inadequate to describe the productivity of the region with any precision. Even in the north equatorial region where our coverage is best, we

have only one series of observations made during the summer months. The fine structure and day-to-day variability in productivity remain to be examined in detail. Sampling errors have been estimated only in a few rather inadequate experiments. All of these gaps in our knowledge prevent us from making realistic estimates of the daily, seasonal, or annual production in any one of the areas included in the present summary.

3. It is likewise evident that the variability in productivity (and of other biological parameters) within even any one of the regions is such that it will be difficult to construct mathematical models relating a number of variables which predict more than the obvious and aid us in understanding more than is already apparent. Frequently the differences we will be looking for will be less than the noise of the system; we desperately need new techniques and additional experimentation, both in the laboratory and in the sea, before we will be able to understand and interpret the interrelationship between and within the biotic and abiotic environments.

In conclusion, it is quite apparent from this, and probably the other two papers dealing with the productivity of the Pacific Ocean, that the number of measurements of primary production and related variables is still inadequate and at present allows only the vaguest notion of the rate of primary production in this ocean area.

Abbreviations and Notations Used in Tables

Hydro. cast depth – m: Depth of the deepest water bottle in cast
I.R.: Incident radiation
O_2: Dissolved oxygen
PO_4 or PO_4-P: Inorganic phosphorus
NO_2: Nitrite determination
NO_3: Nitrate determination
pH: Hydrogen ion concentration
Alk.: Alkalinity
Si: Silicate
CO_2: Carbon dioxide
Opt. Meas.: Optical measurements
k: Attenuation coefficient
Chloro.: Chlorophyll
NAC: Non-astacin carotenoids
AC: Astacin carotenoids
obl. or o: Oblique tow
S: Surface tow
c: Horizontal closing tow
c-B: Clarke-Bumpus horizontal tow
Surf.: Surface determination
Water Col.: Measurement at one or more depths below the surface
i.s.: *in situ* measurement
l.i.: Laboratory-type photosynthesis incubator, using artificial illumination
d.i.: Deck-type photosynthesis incubator, using natural illumination
P.S. layer depth – m: Depth of the photosynthetic layer estimated

NOTE: Vityaz 29: A variety of nets and trawls was used in this cruise, and the notations used are similar to those appearing in the original data sheets obtained from the World Data Center. The notation is clarified at the end of the Vityaz 29 summary.

Table 1—AREA: NORTH EQUATORIAL: OFFSHORE

Bennett, E. and M. B. Schaefer. Studies of physical, chemical and biological oceanography in the vicinity of the Revilla Gigedo Islands during the "Island Current Survey" of 1957. I.A.T.T.C. Bull. IV, No. 5, 1960.

				Hydro. Cast	Chemistry				Chlorophyll a		Productivity			
										Water	Surf.		Water Col.	
Sta. No.	Date 1957	Lat. N.	Long. W.	Depth-m	O_2	PO_4	NO_2	Zoopl.	Surf.	Col.	i.s.	li.	i.s.	li.
1	May 12	18°14′	114°44′	2129	-	x	x	Obl.	x	x				
2	13	19°24′	115°43′	249a	x	x	x	Obl.	x	x				
4	13	19°32′	114°56′	1179	x	x	x	Obl.		x	x	x	x	x
6	14	19°24′	113°37′	253a	x	x	x	Obl.	x	x				
7	14-15	18°26′	113°36′	2207	x	x	x	Obl.	x	x	x	x	x	x
9	15	18°14′	114°38′	50a	x	x	x	Obl.	x	x				
11	15	18°22′	115°44′	835	x	x	x	Obl.	x	x	x	x	x	x
12	16	17°22′	115°43′	1914	x	x		Obl.	x	x				
14	16	17°18′	114°41′	1194	x	x		Obl.	x	x	x	x	x	x
16	17	17°24′	113°30′	2248	x	x		Obl.	x	x				
17	20	18°22′	114°42′	21	x	x	x		x					
18	20	18°22′	114°42′	31	x	x	x		x					
19	20	18°21′	114°41′	54	x	x	x		x	x				
20	20	18°21′	114°40′	100	x	x	x		x	-				
21	20	18°21′	114°39′	823	x	x	x	Obl.	x	x				
22	21	18°19′	114°44′	80		x	x		x					
23	21	18°19′	114°47′	80		x	x		x					
24	21	18°25′	114°48′	80		x	x		x					
25	21	18°24′	114°44′	80		x	x		x					
27	22	18°20′	114°41′	80		x	x		x					
28	22	18°21′	114°40′	102	x	x	x		x	x	x	x	x	x
29	23	18°18′	114°48′	894					x	x				
30	23	18°21′	114°46′	26	x	x	x		x					
31	23	18°21′	114°46′	28	x	x	x		x					
32	23	18°20′	114°48′	60	x	x	x		x	x				
33	24	18°21′	114°48′	76	x	x	x		x	x				
34	24	18°21′	114°46′	30	x	x		Obl.	x	x	x	x	x	x
35	24	18°21′	114°44′	-					x	x	x	x	x	x
37	25	18°22′	114°46′	20	x	x	x		x					
38	25	18°22′	114°47′	25	x	x	x		x					
39	25	18°23′	114°47′	63	x	x	x		x	x				
40	25	18°24′	114°48′	89	x	x	x		x	x				
42	May 27	18°29′	114°42′	1128	x	x	x	Obl.	x	x	x	x	x	x
43	27	18°23′	114°41′	30	x	x	x		x					
44	27	18°23′	114°41′	45	x	x	x		x	x				

45	27	18°24′	114°41′	80	x	x	x		x	x				
46	28	18°25′	114°42′	20a	x	x	x		x	x				
47	28	18°20′	114°48′	510	x		x	Obl.	x	x	x	x	x	x
51	June 2	16°50′	117°30′	1127	x	x	x	Obl.	x	x				
53	2	16°51′	117°30′	462	x	x	x	Obl.	x	x				
54	2	16°51′	117°30′	70	x	x	x		x	x				
55	2	16°52′	117°30′	60	x	x	x		x					
56	3	16°53′	117°30′	150	x	x	x		x	x				
57	3	16°53′	117°30′	493	x	x	x	Obl.	x	x				
59	3	16°55′	117°30′	1130	x	x	x	Obl.	x	x	x	x	x	x
60	4	16°52′	117°28′	1127	x	x	x		x	x				
61	4	16°52′	117°29′	231	x	x	x		x	x				
62	4	16°52′	117°30′	40	x	x	x		x					
63	5	16°52′	117°31′	356	x	x	x		x	x				
64	5	16°52′	117°32′	1132	x	x	x	Obl.	x					
65	5	18°52′	117°30′	75	x	x	x	Obl.	x	x	x	x	x	x
67	8	18°43′	110°57′	20	x	x			x					
70	8	18°40′	110°56′	100	x	x	x	Obl.	x	x				
71	8	18°49′	111°04′	30	x	x			x					
73	8	18°50′	111°06′	100	x	x	x	Obl.	x	x				
74	9	18°49′	110°56′	30	x	x			x					
76	9	18°50′	110°54′	99	x	x	x	Obl.	x	x				
80	10	22°52′	113°11′					Obl.	x	x				
81	10	22°59′	114°13′						x	x				
82	10	23°04′	113°13′					Obl.	x	x				
	May 10	27°20′	116°09′						x					
	10	25°15′	115°50′						x					
	10	25°18′	115°50′								x			
	10	24°47′	115°55′						x		x			
	11	22°45′	115°21′								x			
	11	21°35′	115°31′								x			
	11	25°00′	115°43′						x					
	11	24°41′	115°46′						x					
	11	22°40′	115°20′						x					
	12	20°33′	115°04′						x					
	12	18°44′	114°48′								x			
	12	18°38′	114°46′						x					
	29	18°19′	114°44′						x					
	30	18°19′	114°44′						x					
	31	18°19′	114°44′						x					
	June 9	21°16′	112°16′								x			
	9	21°16′	112°15′						x					

a. Pretrip below this depth.

Table 2—AREA: NORTH EQUATORIAL, NORTH: INSHORE AND OFFSHORE

Blackburn, M., et al. Physical, chemical, and biological observations in the eastern tropical Pacific Ocean: three cruises to the Gulf of Tehuantepec, 1958-1959. S.S.R., Fisheries No. , U.S.F.W.S. Washington, D. C. 1961.

				Hydro. Cast		Chemistry								Phytoplankton						
														Chlor.a		Productivity				
																Surface			Water Col.	
Sta. No.	Date 1958	Lat. N.	Long. W.	Depth m	I. R.	Dis. O_2	PO_4 -P	Tot. PO_4	NO_2	NO_3	Opt. Meas.	Nek-ton	Zoopl.	Surf.	Water Col.	i.s.	li.	di.	i.s.	li.
A-2	Nov. 2	25°39′	113°26′											x			x			
B-2	3	25°22′	114°04′											x			x			
C-2	4	23°04′	110°20′											x						
D-1	5	20°02′	107°26′											x			x			
E-23	6	17°14′	104°07′											x			x	x		
F-23	7	15°30′	100°13′											x			x	x		
G	8	14°31′	95°42′														x	x		
2	22	13°37′	92°57′	971	x	x	x						obl.	x	x		x	x		x
6	23	14°59′	94°01′	199	x	x	x						obl.	x	x					
9	24	13°39′	94°52′	995	x	x	x				K		obl.	x	x		x			x
15	28	14°55′	95°59′	984	x	x	x				K		obl.	x	x		x	x		x
20	30	15°07′	96°55′	965	x	x	x				K			x	x		x	x		x
23	Dec. 1	15°36′	99°23′	946	x	x	x				K		obl.				x	x		x
25	2	16°58′	102°28′	666	x	x	x						obl.	x	x					
31	6	25°36′	113°18′		x											x			x	
	1959																			
2	Jan. 17	27°12′	114°40′	108	x	x	x				K		o,c	x	x		x			x
4	18	25°05′	112°55′	452	x	x	x				K		o,c	x	x		x			x
6	19	23°14′	110°41′	789	x	x	x				K		o,c	x	x	x	x	x		x
8	20	21°17′	108°16′	1089	x	x	x				K		o,c	x	x	x	x	x		x
10	21	19°34′	106°03′	1080	x	x	x						o,c	x	x	x	x	x		x
12	22	18°10′	103°26′	1014	x	x	x				K		o,c	x	x	x	x	x		x
14	27	14°40′	97°44′	1006	x	x	x				K		o,c	x	x		x			x
16-1	28	14°38′	97°01′											x			x	x		
19-1	29	15°14′	96°06′											x			x	x		
23	30	13°49′	94°57′	1128	x	x	x				K		o,c	x	x		x	x		x
24-22	Feb. 6	14°42′	94°44′											x				x		
27	7	14°01′	92°23′	200	x	x	x	x			K		o,c	x	x		x	x		x
29	8	11°40′	90°53′	652	x	x	x	x			K		o	x	x		x	x		x
29-2	8	11°10′	90°27′											x						
29-4	8	11°02′	90°22′											x						
29-6	8	10°50′	90°19′											x						
29-8	9	10°38′	90°16′											x						

29-12	9	10°15′	90°09′											x						
29-14	9	10°06′	90°06′											x						
29-16	9	9°56′	89°57′											x						
29-18	9	9°46′	89°48′											x						
29-20	9	9°38′	89°41′											x						
29-22	9	9°27′	89°39′											x						
29-24	9	9°18′	89°20′											x						
29-26	9	9°09′	89°12′											x						
29-28	9	8°57′	89°02′											x						
29-30	9	8°47′	88°52′											x						
29-32	10	8°36′	88°42′											x						
29-34	10	8°26′	88°31′											x						
29-36	10	8°16′	88°21											x						
29-38	10	8°06′	88°11′											x						
30	10	8°10′	88°06′	1086	x	x	x	x			K		o,c	x	x		x	x		x
31	10	8°36′	88°16′	399	x	x	x						o	x						
32	11	8°58′	88°22′	496	x	x	x					obl.	s,o,c	x						
33	11	9°49′	88°32′		x								o	x						
33-1	11	10°04′	88°33′											x			x			
35	13	12°06′	89°36′	173	x	x	x	x			K		o	x	x		x			x
37	14	14°12′	92°35′	258	x	x	x	x			K		o,c	x	x	x	x	x	x	x
40	16	15°51′	97°58′	729	x	x	x	x			K		s,o,c	x	x		x			
42	17	16°42′	100°12′	1018	x	x	x	x			K		o,c	x	x	x	x	x	x	x
44	18	17°47′	103°14′	1093	x	x	x	x			K		o	x	x		x	x		x
46	20	19°46′	105°44′	1094	x	x	x	x			K	obl.	s,o,c	x	x	x	x	x	x	x
47	20	20°41′	107°10′	1095	x	x		x			K		o	x	x		x	x		x
49	21	22°42′	109°50′	1093		x		x			K		o	x	x		x	x		x
51	22	24°58′	112°36′	41	x	x		x			K		s,c	x	x	x	x	x	x	x
2	Aug. 16	26°19′	113°52′	250	x	x	x					obl.	o	x	x					
5	16	25°44′	114°42′	625	x	x	x		x	x			o	x	x		x	x		
8	17	25°19′	115°43′		x							obl.	o	x	x					
10	17	24°31′	115°45′	502	x	x	x						o	x	x		x	x		
13	17	25°06′	114°43′		x							obl.	o	x	x					
16	18	25°35′	113°44′	517	x	x	x		x	x			o	x	x		x	x		
20	19	25°34′	113°22′	123	x	x	x		x	x	K		o	x	x	x	x	x	x	x
21	20	25°00′	113°24′	602	x	x	x						o	x	x					
24	20	24°29′	114°22′	601	x	x	x				K		o	x	x		x			
30	22	25°14′	113°03′	404	x	x	x				K		o	x	x		x	x		
32	23	24°26′	113°02′	603	x	x	x					obl.	o	x	x					
34	23	24°08′	113°42′	567	x	x	x		x	x	K		o	x	x					
38	24	23°26′	114°55′	533	x	x	x			x		obl.	o	x	x					
39	24	22°50′	114°32′	396	x	x	x				K		o	x	x					
42	24-25	23°20′	113°40′		x							obl.	s,o	x	x					
45	25	23°51′	112°40′	581	x	x					K		o	x	x					

Table 2—AREA: NORTH EQUATORIAL, NORTH: INSHORE AND OFFSHORE (Cont'd.)

				Hydro. Cast Depth		Chemistry								Phytoplankton						
														Chlor.a		Productivity				
																Surface			Water Col.	
Sta. No.	Date 1959	Lat. N.	Long. W.	m	I. R.	Dis. O_2	PO_4 -P	Tot. PO_4	NO_2	NO_3	Opt. Meas.	Nek-ton	Zoopl.	Surf.	Water Col.	i.s.	li.	di.	i.s.	li.
49	26	23°36′	111°49′	598	x	x	x		x	x	K		o	x	x					
52	26-27	23°10′	112°40′		x							obl.	o	x	x					
55	27	22°40′	113°35′	601	x	x	x				K		o	x	x					
58	28	22°28′	112°32′	602		x	x					obl.	o	x	x					
61	28	22°54′	111°42′	597	x	x	x				K		o	x	x					
64	29	23°24′	110°39′	300	x	x	x					obl.	o	x	x					
66	29	22°46′	110°22′	499	x	x	x				K			x	x					
68	Sept. 4	18°39′	103°59′	205		x	x		x	x	K		o	x	x	x	x		x	x
70	7	15°00′	97°00′	1116	x	x	x				K		o,c	x	x		x	x		
73	8	13°42′	95°56′	1148		x	x				K		o	x	x		x	x		
74	9	14°20′	95°59′	1125		x	x					obl.	s,o	x	x					
76	9	15°35′	96°02′	1019	x	x	x				K		o,c	x	x		x	x		
77	10	15°42′	95°54′	188	x	x	x				K			x	x		x	x		
81	11	13°40′	95°00′	1174		x	x				K		o,c	x	x		x	x		
82	12	13°40′	94°00′	1186		x	x					obl.	o	x	x					
84	14	16°28′	99°32′	1043		x	x					obl.	s,o,c	x	x					
85	15-16	17°10′	101°17′									obl.	s,o,c	x	x					
86	16-17	18°40′	104°09′		x							obl.	o,c	x	x					
87	18	20°09′	106°32′	1178	x	x	x					obl.	s,o,c	x	x					
88	18-19	22°00′	109°04′		x							obl.	s,o,c	x	x					
89	19-20	24°16′	111°60′									obl.	s,o,c	x	x					

Table 3—AREA: NORTH, NORTH EQUATORIAL: INSHORE AND OFFSHORE

Doty, M. Unpublished. Information supplied on I.B.M. sheets

						PHYTOPLANKTON									
					Hydro. Cast	Chlorophylls						Productivity			
					Depth	Surface			Water			Surface	Water		Tech-
Cruise	Sta. No.	Date 1952	Lat. N.	Long. W.	m	a	b	c	Col.a	NAC	AC	li.	Col. li.	Method*	nique†
D-01	698	Mar. 31	26°52′	148°32′								x			O
	699	Apr. 3	33°37′	134°53′								x	x		O
	700	4	35°45′	129°10′								x	x		O
	701	5	37°16′	124°36′								x	x		O
	705	22	32°50′	117°32′								x			O
	707	24	26°00′	113°31′								x	x		O
	708	25	22°50′	110°06′								x	x		O
	709	26	20°00′	106°12′								x	x		O
	715	May 4	13°00′	95°48′								x	x		O
	717	7	08°41′	86°12′								x	x		O
	719	10	06°52′	79°30′								x			O
	720	11	05°36′	79°31′								x	x		O
	723	12	06°00′	79°54′								x			O
	755	22	11°52′	77°41′								x	x		O
	756	24	15°00′	71°06′								x	x		O
		1955													
S-01	1	Oct. 2	29°53′	116°50′		x						x			O
	3	3	26°00′	116°43′		x									
	4	4	24°02′	116°31′		x									
	6	5	20°09′	116°16′		x						x			O
	8	6	16°31′	116°13′		x									
	10	7	14°01′	116°13′		x									
	13	8	11°02′	116°05′		x						x			O
	15	9	09°06′	115°44′		x									
	18	10	05°58′	115°43′		x									
	19	10	05°00′	115°36′		x						x			O
	21	11	03°05′	115°44′		x									
	23	12	00°58′	116°03′		x									
	24	13	00°04′	115°39′		x						x	x		O
	25	17	06°00′	115°24′		x									
	27	18	08°02′	115°40′		x			x			x			O
	30	19	10°58′	115°58′		x									

Table 3—AREA: NORTH, NORTH EQUATORIAL: INSHORE AND OFFSHORE (Cont'd.)

Cruise	Sta. No.	Date 1955	Lat. N.	Long. W.	Hydro. Cast Depth m	PHYTOPLANKTON Chlorophylls Surface a	b	c	Water Col. a	NAC	AC	Productivity Surface li.	Water Col. li.	Method*	Tech-nique†
		20	09°50′	115°56′		x									
		21	10°41′	115°32′		x			x			x	x		O
S-01		22	08°43′	113°22′		x									
		23	07°36′	111°21′		x									
		24	08°39′	111°12′		x									
		25	09°29′	111°12′		x									
31	3	25	15°36′	105°36′								x		5	O
31	4	26	12°01′	106°57′		x	x	x		x	x	x		5	O
S-01		26	09°31′	109°27′		x									
		27	09°35′	105°35′		x									
31	5	27	08°25′	108°16′		x	x	x			x	x		5	O
S-01		28	09°57′	101°33′		x			x			x			O
		29	09°56′	96°45′		x									
		30	08°53′	92°38′		x									
		31	11°05′	88°58′		x									
		Nov. 1	07°54′	87°01′		x									
		2	09°21′	88°08′		x									
	33	3	10°39′	89°51′		x			x			x	x		O
	35	4	09°27′	87°53′		x			x			x	x		O
	37	5	07°33′	87°21′		x			x			x	x		O
	39	6	07°51′	84°34′		x			x			x	x		O
	41	7	09°13′	84°51′		x									
	42	11	08°54′	84°41′		x									
	45	12	06°04′	84°09′		x						x			O
		13	03°20′	83°53′		x									
	50	14	00°57′	83°49′		x									
		16	01°13′S	83°51′		x									
	55	17	03°42′	83°06′		x						x			O
		21	02°48′	84°12′		x									
	56	21	01°59′	83°20′		x									
	227	23	01°48′	84°46′		x									
	57	23	04°03′	84°11′		x			x			x	x		O
		24	01°57′	87°13′		x									
	59	28	01°06′	91°31′		x									

	62	29	03°49′	90°37′	x								
	65	30	07°01′	89°39′	x								
	67	Dec. 1	08°53′	89°35′	x								
		2	14°11′	93°15′	x								
S-01	69	2	11°02′	88°46′	x								
		7	12°51′	90°17′	x								
		9	14°41′	95°42′	x								
	87	10	14°02′	98°42′	x								
	89	11	15°58′	101°31′	x								
S-01	317	12	18°07′	104°03′	x								
		13	20°29′	106°40′	x								
		14	22°40′	109°41′	x								
		1956											
33	0	Mar. 6	14°56′	148°08′						x		5	O
	0	6	15°09′	148°53′						x		5	O
	0	6	15°09′	148°53′						?	x	5	CR
	0	6	15°26′	149°26′						x		5	O
	0	9	10°52′	139°57′						x		5	O
	0	9	10°52′	139°57′							x	5	CR
	0	9	11°56′	140°02′						x		5	O
	0	9	11°56′	140°02′						?	?	5	CR
	0	28	10°25′	147°57′						x		5	O
	0	29	11°59′	149°10′						x		5	O
35	4	Aug. 10	17°11′	149°29′						x		5	O
	5	10	16°43′	148°02′						x		5	O
	6	11	16°29′	146°30′						x		5	O
	7	11	15°57′	145°10′						x		5	O
	8	12	15°05′	143°35′						x		5	O
	9	12	14°30′	142°09′						x		5	O
	10	13	14°05′	140°33′						x		5	O
	11	13	13°40′	139°08′						x		5	O
	12	14	13°04′	137°27′						x		5	O
	13	14	12°27′	135°54′						x		5	O
	14	15	11°09′	135°00′						x		5	O
31	64	Oct. 27	07°06′	108°36′						x		5	O
	66	28	05°52′	109°05′	x	x	x	x	x	x		5	O
	67	28	04°39′	109°24′						x		5	O
	69	29	03°13′	110°12′	x	x	x	x	x	x		5	O
	70	29	02°14′	110°55						x		5	O
	72	30	01°04′	111°33′	x	x	x	x	x	x		5	O
	73	30	00°12′S	112°25′						x		5	O
	75	31	01°23′	112°46′	x	x	x	x	x	x		5	O

Table 3—AREA: NORTH, NORTH EQUATORIAL: INSHORE AND OFFSHORE (Cont'd.)

						PHYTOPLANKTON									
					Hydro. Cast	Chlorophylls						Productivity			
					Depth	Surface			Water			Surface	Water		Tech-
Cruise	Sta. No.	Date 1956	Lat. N.	Long. W.	m	a	b	c	Col. a	NAC	AC	li.	Col. li.	Method*	nique†
	76	31	02°54′	113°08′								x		5	O
	78	Nov. 1	04°24′	113°00′		x	x	x		x		x		5	O
	79	1	05°24′	113°18′								x		5	O
	81	2	06°37′	113°56′		x	x	x		x	x	x		5	O
	82	2	07°37′	114°48′								x		5	O
	84	3	07°49′	116°47′		x	x	x		x	x	x		5	O
	85	4	07°56′	120°04′		x	x	x		x	x	x		5	O
	86	4	06°43′	120°06′								x		5	O
	88	5	05°14′	120°08′		x	x	x		x	x	x		5	O
	89	5	04°13′	120°06′								x		5	O
	91	6	02°48′	120°06′		x	x	x			x	x		5	O
	92	6	01°32′	120°05′								x		5	O
	94	7	00°11′	119°58′		x	x	x		x	x	x		5	O
	0	7	01°06′	120°00′								x		5	O
	97	8	02°44′	120°02′		x	x	x		x	x	x		5	O
	99	8	04°00′	120°12′								x		5	O
	101	8	03°58′	120°20′		x	x	x		x	x	x		5	O
	103	8	04°06′	120°24′								x		5	O
	108	9	04°48′	120°08′		x	x	x		x	x	x		5	O
	109	9	06°04′	120°00′								x		5	O
	111	10	05°10′	121°20′		x	x	x		x	x	x		5	O
	114	11	03°01′	123°47′		x	x	x		x	x	x		5	O
	117	12	01°19′	126°17′		x	x	x		x	x	x		5	O
	120	13	00°25′S	128°28′		x	x	x		x	x	x		5	O
		1957													
38	2	Jan. 15	14°00′	147°24′								x		5	O
	3	16	12°07′	144°29′		x		x		x	x	x		5	O
	4	17	10°25′	141°24′		x	x	x		x	x	x		5	O
	8	21	02°53′	129°06′		x	x	x		x	x	x		5	O
	9	22	00°45′	126°05′		x	x	x		x	x	x		5	O
	10	23	00°04′	123°57′		x	x	x		x	x	x		5	O
	11	24	00°24′	119°50′		x	x	x		x	x	x		5	O
	12	25	00°15′S	116°49′		x	x	x		x	x	x		5	O
	13	26	00°07′	113°27′		x	x	x		x	x	x		5	O

	14	27	00°12′	110°12′	x	x	x	x	x	x	5	O
	15	28	03°24′	110°01′	x	x	x	x	x	x	5	O
	16	29	06°58′	110°01′	x	x	x	x	x	x	5	O
	17	30	10°11′	109°59′	x	x	x	x	x	x	5	O
	18	31	13°06′	110°03′	x	x	x	x	x	x	5	O
	19	Feb. 1	13°32′	110°12′	x	x	x	x	x	x	5	O
	20	3	13°39′	110°39′	x	x	x	x	x	x	5	O
	21	4	13°38′	111°02′	x	x	x	x	x	x	5	O
	22	5	13°45′	111°15′	x	x	x	x	x	x	5	O
	23	6	13°48′	111°48′	x	x	x	x	x	x	5	O
	24	7	13°55′	112°01′	x	x	x	x	x	x	5	O
	25	8	14°06′	112°17′	x	x	x	x	x	x	5	O
	26	9	14°11′	112°33′	x	x	x	x	x	x	5	O
	27	10	14°13′	112°45′	x	x	x		x	x	5	O
	28	11	14°15′	112°59′	x	x	x	x	x	x	5	O
	29	12	14°17′	113°12′						x	5	O
	30	15	14°23′	114°07′	x	x	x	x	x	x	5	O
	31	16	14°18′	114°28′	x	x	x	x	x	x	5	O
	32	18	14°00′	116°35′	x	x	x	x	x	x	5	O
	33	19	13°36′	118°21′	x	x	x	x	x	x	5	O
	34	25	01°35′	129°51′	x	x	x	x	x	x	5	O
	37	28	11°48′	129°58′	x	x	x	x	x	x	5	O
	39	Mar. 1	15°22′	129°53′	x	x	x	x	x	x	5	O
		1959										
52	5	May 1	27°49′	149°47′						x	5	O
	7	2	30°21′	146°41′						x	5	O
	9	3	32°37′	143°31′						x	5	O
	11	4	34°23′	141°13′						x	5	O
	12	5	34°48′	140°41′						x	5	O
	12	55	34°48′	140°41′						x	5	CR
	13	5	35°17′	140°13′						x	5	O
	15	6	36°48′	138°00′						x	5	O
	17	7	38°28′	135°50′						x	5	O
	18	8	38°48′	135°06′						x	5	O
	21	9	36°40′	132°21′						x	5	O
	22	10	36°21′	131°55′						x	5	O
	22	10	36°21′	131°55′						x	5	CR
	24	11	34°32′	129°32′						x	5	O
	24	11	34°32′	129°32′						x	5	CR
	25	12	34°36′	126°54′						x	5	O
	25	13	37°24′	123°02′						x	5	O

Table 3—AREA: NORTH, NORTH EQUATORIAL: INSHORE AND OFFSHORE (Cont'd.)

						PHYTOPLANKTON									
					Hydro. Cast Depth	Chlorophylls						Productivity			
						Surface			Water			Surface	Water		Tech-
Cruise	Sta. No.	Date 1959	Lat. N.	Long. W.	m	a	b	c	Col. a	NAC	AC	li.	Col. li.	Method*	nique†
	26	17	33°19′	128°00′								x		5	O
	28	18	31°26′	125°32′								x		5	O
	28	18	31°26′	125°32′								x		5	CR
	29	19	29°25′	124°02′								x		5	O
	29	20	29°39′	123°56′								x		5	O
	29	20	29°39′	123°56′								x		5	CR
	30	21	28°53′	128°24′								x		5	O
	32	22	27°21′	122°07′								x		5	O
	33	23	26°59′	121°59′								x		5	O
	33	23	26°59′	121°59′								x		5	CR
	34	23	26°51′	121°32′								x		5	O
	34	23	26°51′	121°32′								x		5	CR
	36	24	27°00′	120°18′								x		5	O
	36	24	27°00′	120°18′								x		5	CR
	38	25	27°04′	118°53′								x		5	O
	38	25	27°04′	118°53′								x		5	CR
	40	26	29°52′	117°58′								x		5	O
	43	30	32°30′	117°46′								x		5	O
	43	30	32°30′	117°46′								x		5	CR
	44	31	32°33′	118°26′								x		5	O
	44	31	32°33′	118°26′								x		5	CR
	45	31	32°33′	119°07′								x		5	O
	45	31	32°33′	119°07′								x		5	CR
	46	June 1	32°05′	119°28′								x		5	O
	46	1	32°05′	119°28′								x		5	CR
	47	1	32°04′	120°05′								x		5	O
	47	1	32°04′	120°05′								x		5	CR
	49	2	31°49′	123°34′								x		5	O
	49	2	31°49′	123°34′								x		5	CR
	51	3	31°03′	124°54′								x		5	O
	53	4	30°39′	124°18′								x		5	O
	53	4	30°39′	124°18′								x		5	CR
	55	5	30°20′	123°05′								x		5	O
	57	6	29°59′	120°57′								x		5	O

59	7	29°48′	118°37′	x	5	O
409	7	35°46′	125°59′	x	5	O
59	8	29°28′	117°55′	x	5	O
60	8	29°28′	117°55′	x	5	O
411	8	34°06′	126°27′	x	5	O
62	9	28°57′	118°01′	x	5	O
62	9	28°57′	118°01′	x	5	CR
414	9	32°12′	127°43′	x	5	O
64	10	29°09′	117°18′	x	5	O
64	10	29°09′	117°18′	x	5	CR
416	10	33°28′	128°14′	x	5	O
65	11	29°23′	117°00′	x	5	O
66	11	28°57′	117°15′	x	5	O
418	11	35°02′	128°27′	x	5	O
68	12	28°14′	119°31′	x	5	O
420	12	36°12′	128°28′	x	5	O
70	13	27°33′	121°45′	x	5	O
422	13	37°29′	128°10′	x	5	O
72	14	27°42′	122°00′	x	5	O
424	14	36°19′	127°26′	x	5	O
74	15	29°55′	120°20′	x	5	O
426	15	34°49′	126°04′	x	5	O
76	16	30°48′	119°16′	x	5	O
77	17	30°47′	119°10′	x	5	O
430	17	32°25′	123°56′	x	5	O
79	18	31°38′	118°15′	x	5	O
432	18	33°18′	124°09′	x	5	O
80	19	31°59′	117°46′	x	5	O
434	19	34°13′	124°22′	x	5	O
436	20	34°11′	124°40′	x	5	O
438	21	35°28′	124°05′	x	5	O
440	22	33°48′	123°06′	x	5	O
443	23	32°51′	122°37′	x	5	O

*Method of obtaining data
5 = Computed by Hawaii IBM program.

† Technique used
O = Standard technique for the cruise.
CR = Some sort of an experiment. The data should not be used for horizontal plots without allowance for the experimental conditions.

Table 4—AREA: SOUTH EQUATORIAL, NORTH EQUATORIAL, NORTH: INSHORE AND OFFSHORE

Holmes, R. W., et al. Primary production, chlorophyll, and zooplankton volumes in the tropical eastern Pacific Ocean. I.A.T.T.C. Bull. 11, 4. La Jolla, Calif., 1957.

							PHYTOPLANKTON					
							Chlorophyll a		Productivity			
				Hydro. Cast	Dis.				Surface		Water Col.	
Sta. No.	Date 1955	Lat. N.	Long. W.	Depth-m	O_2	Zoopl.	Surface	Water Col.	i.s.	li.	i.s.	li.
1	Oct. 2	29°53′	116°50′		x		x		x			
3	3	26°00′	116°43′		x		x					
4	4	24°02′	116°31′	305	x	obl.	x					
6	5	20°09′	116°16′	330	x	obl.	x		x	x		
8	6	16°31′	116°13′	380	x	obl.	x					
10	7	14°01′	116°13′	291	x	obl.	x					
13	8	11°02′	116°05′	330	x	obl.	x		x	x		
15	9	9°06′	115°44′	308	x	obl.	x					
18	10	5°58′	115°43′	331	x	obl.	x					
19	10	5°00′	115°36′	325	x	obl.	x			x		
21	11	3°05′	115°44′	321	x	obl.	x					
23	12	0°58′	116°03′	168	x	obl.	x					
24	13	0°04′	115°39′	300	x	obl.	x		x	x	x	x
25	17	6°00′	115°24′	322		obl.	x					
27	18	8°02′	115°40′	297		obl.	x	x	x	x		
30	19	10°58′	115°58′	308		obl.	x					
28-3	20	9°50′	115°56′				x					
31-11	21	10°41′	115°32′				x	x	x	x	x	x
31-22	22	8°43′	113°22				x					
A-4	23	7°36′	111°21′				x					
A-5	24	8°39′	111°12′				x					
A-6	25	9°29′	111°12′				x					
31-50	26	9°31′	109°27′				x					
	27	9°35′	105°35′				x					
32-10	28	9°57′	101°33′				x	x	x	x		
32-17	29	9°56′	96°45′				x					
32-26	30	8°53′	92°38′				x					
32-38	31	11°05′	88°58′				x					
32-51	Nov. 1	7°54′	87°01′				x					
32-62	2	9°21′	88°08′				x					
33	3	10°39′	89°51′	293	x	obl.	x	x	x	x	x	x
35	4	9°27′	87°53′	323	x	obl.	x	x	x	x	x	x
37	5	7°33′	87°21′	307	x	obl.	x	x	x	x	x	x
39	6	7°51′	84°34′		x		x	x	x		x	
41	7	9°13′	84°51′		x		x					
42	11	8°54′	84°41′	296	x	obl.	x					
45	12	6°04′	84°09′	314	x	obl.	x		x	x		
47-2	13	3°20′	83°53′				x					
50	14	0°57′	83°49′	318	x	obl.	x					
51	15	0°00′	83°47′	280	x	obl.	x		x	x		
52-1	16	1°13′S	83°51′				x					
55	17	3°42′S	83°06′	314	x	obl.	x			x		
56	21	1°59′S	83°20′	293	x	obl.	x					
A-11	21	2°48′S	84°12′				x					
57	23	4°03′S	84°11′	289	x	obl.	x	x	x	x	x	x
227	23	1°48′S	84°46′				x					
W-1	24	1°57′S	87°13′				x					
59	28	1°06′	91°31′	318	x	obl.	x					
62	29	3°49′	90°37′	274	x	obl.	x					
65	Nov. 30	7°01′	89°39′	292	x	obl.	x					
67	Dec. 1	8°53′	89°35′	298	x	obl.	x					
69	2	11°02′	88°46′	263		obl.	x					
77-1	7	12°51′	90°17′				x					
80-1	8	14°11′	93°15′				x					
	9	14°41′	95°42′				x					
87	10	14°02′	98°42′	292		obl.	x					
89	11	15°58′	101°31′	298		obl.	x					
317	12	18°07′	104°03′				x					
91-4	13	20°29′	106°40′				x					
	14	22°40′	109°41′				x					

Table 5—AREA: NORTH EQUATORIAL, NORTH: INSHORE AND OFFSHORE

Holmes, R. W., et al. Physical, chemical, and biological oceanographic observations obtained on Expedition SCOPE in the eastern tropical Pacific November-December 1956. S.S.R., Fisheries No. 279, U.S.F.W.S. Washington, D. C. 1958.

													PHYTOPLANKTON						
				Hydro. Cast	Chemistry								Chlor. a		Productivity				
				Depth		Dis.	PO_4				Opt.			Water	Surface			Water Col.	
Sta. No.	Date 1956	Lat. N.	Long. W.	m	I.R.	O_2	-P	NO_2	pH	Alk.	Meas.	Zoopl.	Surf.	Col.	i.s.	li.	di.	i.s.	li.
BT0-1	Nov. 8	30°01′	116°49′										x						
BT0-3	8	28°59′	116°36′										x						
BT0-9	9	25°44′	116°01′				x					obl.	x		x	x			
BT0-11	9	25°33′	115°53′										x			x			
BT0-13	9	25°21′	115°54′									obl.				x			
BT0-15	9	25°08′	115°51′										x		x	x			
BT0-19	9	24°54′	115°42′									obl.	x						
BT0-21	10	24°42′	115°42′				x					obl.	x						
BT0-25	10	23°18′	114°26′				x						x		x				
1	10	22°57′	113°34′	735	x	x	x		x	x		obl.	x	x					
BT1-5	11	21°34′	110°49′				x						x		x	x			
2	11	21°07′	110°03′	734	x	x	x	x	x	x	K	obl.	x	x	x	x			x
BT2-1	12	20°45′	109°20′				x						x						
BT2-5	12	19°46′	107°25′				x						x		x	x			
3	12	19°17′	106°32′	721	x	x	x		x		K	obl.	x	x	x	x			x
BT3-1	13	18°57′	105°59′				x						x						
BT3-5	13	17°54′	103°50′				x						x		x	x			
4	13	17°27′	102°53′	731	x	x	x		x			obl.	x	x	x	x			x
BT4-2	14	16°52′	101°40′										x						
5	14	16°15′	100°28′	728	x	x	x		x	x		obl.	x	x		x			x
BT5-3	15	15°30′	98°59′										x						
BT5-6	15	14°42′	97°29′										x		x	x			
6	15	14°17′	96°34′	536	x	x	x		x			obl.	x	x		x			
BT6-1	16	14°07′	96°25′				x						x						
BT6-5	16	13°15′	95°10′				x						x			x			
7	16	12°41′	94°15′	729	x	x	x		x			obl.	x	x		x			
BT7-1	17	12°34′	93°43′				x						x						
BT7-5	17	11°41′	91°52′				x						x		x				
8	17	11°13′	90°55′	718	x	x	x	x	x	x		obl.	x	x					
BT8-1	18	11°02′	90°25′				x						x						
BT8-5	18	10°16′	88°22′				x						x		x	x			
9	18	08°56′	88°30′		x							obl.	x	x	x	x			
9A	19	08°56′	88°29′	1559	x	x	x	x	x	x		obl.			x	x			x
9C	20	09°15′	89°18′	141	x	x	x	x	x	x	K	obl.	x	x	x	x		x	x
9D	21	09°34′	89°13′	145	x	x	x	x	x		K	obl.	x	x	x	x		x	x
BT9-29	21	09°34′	89°13′												x				
9F	23	09°41′	89°44′	148	x	x	x				K		x	x	x	x		x	x
BT9-42	24	08°58′	87°02′				x								x	x			

Table 5—AREA: NORTH EQUATORIAL, NORTH: INSHORE AND OFFSHORE (Cont'd.)

Holmes, R. W., et al. Physical, chemical, and biological oceanographic observations obtained on Expedition SCOPE in the eastern tropical Pacific November-December 1956. S.S.R., Fisheries No. 279, U.S.F.W.S. Washington, D. C. 1958.

													PHYTOPLANKTON						
				Hydro. Cast Depth		Chemistry							Chlor. a		Productivity				
															Surface			Water Col.	
Sta. No.	Date 1956	Lat. N.	Long. W.	m	I.R.	Dis. O_2	PO_4-P	NO_2	pH	Alk.	Opt. Meas.	Zoopl.	Surf.	Water Col.	i.s.	li.	di.	i.s.	li.
10	24	08°42′	86°01′	736	x	x	x	x	x		K	obl.	x	x	x	x			x
BT10-1	25	08°32′	85°23′				x						x						
BT10-5	25	08°02′	83°24′				x						x		x	x			
11	25	07°37′	82°25′	769	x		x	x	x		K	obl.	x	x		x			x
16	Dec. 1	05°59′	79°49′	720	x	x	x	x	x		K	obl.	x	x	x	x			x
BT16-1	1	05°36′	80°24′				x						x						
BT16-5	2	04°28′	82°36′				x						x		x				
17	2	04°09′	83°34′	743	x	x	x	x	x	x	K	obl.	x	x	x	x			x
BT17-1	3	04°20′	84°06′				x						x						
BT17-5	3	04°58′	86°03′				x						x		x	x			
18	3	05°28′	86°57′	736	x	x	x	x	x	x	K	obl.	x	x	x	x			x
BT18-1	4	05°38′	87°11′				x						x						
BT18-5	4	06°22′	88°59′				x						x		x	x			
19	4	06°46′	89°52′	722	x	x	x	x	x	x	K	obl.	x	x	x	x			x
BT19-1	5	07°08′	90°19′				x						x						
20A	5	07°50′	91°17′	94	x	x	x	x	x	x			x	x	x	x		x	x
BT20-4	5	07°53′	91°21′												x				
20B	6	07°52′	91°19′	1915		x	x	x	x	x	K	obl.	x		x				
BT20-8	6	09°06′	82°43′				x						x		x				
BT20-10	6	09°46′	93°30′										x		x				
BT20-12	7	10°21′	94°16′				x						x						
BT20-16	7	11°26′	95°38′				x						x		x	x			
21	7	12°17′	96°50′	736		x	x	x	x		K	obl.		x					
BT21-5	8	13°47′	99°11′				x						x		x	x			
22	8	14°37′	100°09′	596		x	x	x	x	x	K	obl.	x	x		x			x
BT22-1	9	14°53′	100°33′				x						x						
BT22-5	9	16°12′	102°17′				x						x			x			
23	9	16°52′	103°06′	737		x	x	x	x	x	K	obl.	x	x	x	x			x
BT23-1	10	17°11′	103°25′				x						x						
BT23-6	10	19°08′	105°29′													x			
24	10	19°30′	105°52′	733		x	x	x		x	K	obl.	x	x	x	x			x
BT24-1	11	19°56′	106°24′				x						x						
BT24-5	11	21°21′	108°03′				x						x			x			
BT24-7	11	21°53′	108°52′										x						
BT24-9	12	22°35′	109°48′				x						x						
25A	12	23°31′	111°22′	486		x	x	x		x	K	obl.			x	x		x	x
25B	13	23°31′	111°19′	144		x	x				K		x	x	x			x	

Table 6—AREA: NORTH EQUATORIAL; NORTH: INSHORE AND OFFSHORE

Holmes, R. W., et al. Physical, chemical, and biological observations in the eastern tropical Pacific Ocean SCOT Expedition, April-June, 1958. S.S.R., Fisheries No. 345. Washington, D. C., 1960.

												PHYTOPLANKTON					
				Hydro. Cast		Chemistry						Chlorophyll a		Productivity			
				Depth		Dis.	PO_4	Tot.	Opti.				Water	Surf.		Water Col.	
Sta. No.	Date 1958	Lat. N.	Long. W.	m	I. R.	O_2	-P	PO_4	Meas.	Nekton	Zoopl.	Surf.	Col.	i.s.	li.	i.s.	li.
4	Apr. 26	23°10′	119°42′	1077	x	x	x	x	K		s,o,c	x	x				
6	27	21°13′	117°23′	1045	x	x	x		K		s,o	x	x	x	x		x
8	28	18°41′	114°53′	1101	x	x	x		K	obl.	s,o	x	x	x	x		x
13	29	18°08′	114°32′	1000	x	x	x		K	obl.	s,o	x	x	x	x		x
15	30	15°28′	112°23′	1135	x	x	x				s,o	x	x	x	x		x
17	May 1	13°03′	110°44′	1128	x	x	x		K		s,o	x	x	x	x		x
23	3	10°14′	109°14′	734	x	x	x	x	K		c	x	x	x	x	x	x
28	4	10°22′	106°56′	982	x	x	x		K		s,o	x	x				
30	5	10°14′	103°54′	975	x	x	x		K		s,o		x	x	x		x
32	6	10°08′	100°40′	1143	x	x	x		K		s,o	x	x	x	x		x
34	7	9°44′	97°14′	1140	x	x	x		K		o	x	x		x		x
37	9	5°10′	95°54′	1065	x	x	x		K		s,o	x	x	x	x		x
42	10	6°36′	95°57′	977		x	x				s,o	x	x		x		
45	11	6°52′	94°29′	1057	x	x	x		K		s,o	x	x				
47	12	8°02′	91°32′	1107	x	x	x		K		s,o	x	x				
49	13	9°48′	89°14′	256	x	x	x	x	K	obl.	s,o	x	x	x	x	x	x
50	14	7°42′	88°08′	1025	x	x	x		K		s,o	x	x	x	x		x
56	16	5°32′	86°43′	1136		x	x	x	K	obl.	s,o,c	x	x	x	x	x	x
58	17	5°34′	83°26′	1120		x	x		K		s,o	x	x	x	x		x
60	18	5°31′	79°54′	1060		x	x		K		s,o	x	x				
62	19	5°28′	77°46′	974		x	x	x	K		s,o,c	x	x	x	x	x	x
70	24	7°15′	82°41′	1065	x	x	x		K		s,o	x	x				
72	25	9°30′	85°52′	1062		x	x		K		s,o	x	x	x	x		x
74	26	11°27′	88°44′	458	x	x	x		K		s,o,c	x	x	x	x		x
76	27	13°16′	91°24′	1068	x	x	x		K		s,o	x	x	x	x		x
78	28	14°14′	93°48′	1036		x	x				s,o	x					
79	28	14°38′	93°52′	1061	x	x	x		K		s,o	x	x	x	x		x
82	29	15°48′	94°53′	115		x	x				o	x					
83	29	15°20′	94°55′	525	x	x	x		K		s,o	x	x	x	x		x
86	30	14°14′	95°51′	1016	x	x	x		K		s,o,c	x	x	x	x		x
88	31	15°11′	96°55′	909	x	x	x	x	K		s,o,c	x	x	x	x	x	x
92	June 1	14°40′	96°08′	885		x	x				s,o	x					
95	2	15°36′	98°43′	1052	x				K		s,o	x	x	x	x		x
100	6	16°04′	100°44′	1070	x	x	x				s,o,c	x	x		x		x
104	7	17°03′	101°26′	901	x	x	x				s,o	x	x		x		x
109	8	17°56′	102°48′	146	x		x				s,o	x	x	x	x		x
122	12	17°51′	105°08′	934	x	x	x		K		s,o	x	x	x	x		x
127	13	19°01′	105°34′	1130	x	x	x		K		s,o	x	x	x	x		x
133	14	19°37′	107°37′	1108	x	x	x		K		s,o	x	x	x	x		x
137	15	20°37′	106°20′								s,o	x	x	x	x		x
139	15	21°05′	106°16′	1118	x	x	x		K		s,o						
143	16	22°18′	108°32′	1081	x	x	x		K		s,o	x	x	x	x		x
145	17	23°52′	111°30′	238		x	x		K		s,o	x	x	x	x		x
147	18	26°38	114°10′	1136		x	x		K		s,o	x	x		x		x

Table 7—AREA: NORTH EQUATORIAL (GULF OF PANAMA)

I.A.T.T.C. Progress Report. Gulf of Panama Station. Meteorological, hydrographic and biological data. E. Forsbergh, unpublished.

										PHYTOPLANKTON				
				Hydro. Cast			Chemistry			Chlorophyll a		Productivity*		
Sta. No.	Date 1954	Lat. N.	Long. W.	Depth m	I.R.	Secci Disk	Dis. O_2	PO_4 -P	Zoopl.	Surface	Water Col.	Depth	i.s.	Water Col. i.s.
1	Nov. 29	8°45′	79°23′	38	x		x		obl.					
2	Dec. 24	8°45′	79°23′	34	x		x		obl.			10	x	
	1955													
3	Jan. 11	8°45′	79°23′	34	x		x		obl.			10	x	
4	25	8°45′	79°23′	40	x		x		obl.			10	x	
5	Feb. 8	8°45′	79°23′	38	x		x		obl.			10	x	
6	22	8°45′	79°23′	35	x		x		obl.					
7	Mar. 10	8°45′	79°23′	38	x		x		obl.					
8	23	8°45′	79°23′	38	x		x		obl.					
9	Apr. 5	8°45′	79°23′	35	x		x		obl.					
10	19	8°45′	79°23′	40	x		x		obl.					
11	May 3	8°45′	79°23′	36	x		x		obl.					
12	16	8°45′	79°23′	36	x		x		obl.					
13	30	8°45′	79°23′	40	x		x		obl.					
14	June 13	8°45′	79°23′	42	x		x		obl.					
15	27	8°45′	79°23′	40	x		x		obl.					
16	July 11	8°45′	79°23′	40	x		x	x	obl.					
17	25	8°45′	79°23′	44	x		x	x	obl.					
18	Aug. 8	8°45′	79°23′	38	x		x	x	obl.					
19	22	8°45′	79°23′	40	x		x	x	obl.					
20	Sept. 5	8°45′	79°23′	42			x	x	obl.					
21	19	8°45′	79°23′	40	x		x	x	obl.					
22	Oct. 3	8°45′	79°23′	40			x	x	obl.					
23	19	8°45′	79°23′	39	x		x		obl.					
24	31	8°45′	79°23′	39	x		x		obl.					
25	Nov. 15	8°45′	79°23′	38	x		x	x	obl.					
26	Dec. 1	8°45′	79°23′	38	x		x	x	obl.					
27	12	8°45′	79°23′	40	x		x	x	obl.			10	x	
28	26	8°45′	79°23′	39	x		x	x	obl.					
	1956													
29	Jan. 9	8°45′	79°23′	38			x	x				10	x	
30	23	8°45′	79°23′	39			x	x	obl.			10	x	
31	Feb. 6	8°45′	79°23′	38			x	x	obl.					

32	21	8°45′	79°23′	38			x	x	obl.			10	x
33	Mar. 5	8°45′	79°23′	40			x	x	obl.				
34	21	8°45′	79°23′	40			x	x	obl.			10	x
35	Apr. 2	8°45′	79°23′				x	x	obl.			10	x
36	17	8°45′	79°23′	40			x	x	s,obl.			10	x
37	30	8°45′	79°23′	40			x	x	s				
38	May 14	8°45′	79°23′	40			x	x	s			10	x
39	June 19	8°45′	79°23′	40		x	x	x	obl.			10	x
40	July 2	8°45′	79°23′	40		x	x	x	s			10	x
41	17	8°45′	79°23′	40	x	x	x	x	obl.				
42	31	8°45′	79°23′	40		x	x	x	s			10	x
43	Aug. 13	8°45′	79°23′	40	x	x	x	x	s			10	x
44	27	8°45′	79°23′	40		x	x	x	s			10	x
45	Sept. 11	8°45′	79°23′	40		x	x	x	obl.				
46	24	8°45′	79°23′	39		x	x	x	obl.			10	x
47	Oct. 8	8°45′	79°23′	40		x	x	x	obl.			10	x
48	22	8°45′	79°23′	40	x	x	x	x	s			10	x
49	Nov. 8	8°45′	79°23′	40	x	x	x	x	obl.				
50	19	8°45′	79°23′	35	x	x	x	x	obl.			10	x
51	Dec. 3	8°45′	79°23′	35		x	x	x	s			10	x
52	17	8°45′	79°23′	38	x		x	x	obl.	x	x	10	x
	1957												
53	Jan. 2	8°45′	79°23′	30		x	x	x	obl.	x	x	10	x
54	14	8°45′	79°23′	35	x	x	x	x	obl.		x	10	x
55	29	8°45′	79°23′	36	x	x	x	x	obl.		x	10	x
56	Feb. 11	8°45′	79°23′	36	x	x	x	x	obl.	x	x	10	x
57	25	8°45′	79°23′	36	x	x	x	x	obl.	x	x	10	x
58	Mar. 12	8°45′	79°23′	38	x	x	x	x	obl.	x	x	10	x
59	21	8°45′	79°23′	38		x	x	x	obl.	x	x	10	x
60	Apr. 10	8°45′	79°23′	37	x	x	x		obl.			10	x
61	22	8°45′	79°23′	37	x	x	x		obl.			10	x
62	May 6	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x
63	20	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x
64	June 3	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x
65	20	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x
66	July 4	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x
67	15	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x
68	29	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x
69	Aug. 12	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x
70	26	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x
71	Sept. 9	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x
72	23	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x

Table 7—AREA: NORTH EQUATORIAL (GULF OF PANAMA) (Cont'd.)

Sta. No.	Date 1957	Lat. N.	Long. W.	Hydro. Cast Depth m	I.R.	Secci Disk	Chemistry Dis. O_2	Chemistry PO_4 -P	Zoopl.	PHYTOPLANKTON Chlorophyll a Surface	PHYTOPLANKTON Chlorophyll a Water Col.	PHYTOPLANKTON Productivity* Depth	PHYTOPLANKTON Productivity* i.s.	PHYTOPLANKTON Productivity* Water Col. i.s.
73	Oct. 7	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x	
74	21	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x	
75	Nov. 5	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x	
76	18	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x	
77	Dec. 2	8°45′	79°23′	37	x	x	x	x		x	x	10	x	
78	14	8°45′	79°23′	37	x	x	x		obl.	x	x	10	x	
79	28	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x	
	1958													
80	Jan. 13	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x	
81	27	8°45′	79°23′	37		x	x	x	obl.	x	x	10	x	
82	Feb. 10	8°45′	79°23′	37	x	x	x	x		x	x	10	x	
83	24	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x	
84	Mar. 11	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x	
85	25	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x	
86	Apr. 7	8°45′	79°23′	37	x	x	x	x	obl.	x	x	10	x	
87	28	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
88	May 12	8°45′	79°23′	37		x	x	x	obl.	x	x	0	x	x
89	June 2	8°45′	79°23′	37		x	x	x	obl.	x	x	0	x	x
90	16	8°45′	79°23′	37		x	x			x	x	0	x	x
91	30	8°45′	79°23′	37		x	x		obl.	x	x	0	x	x
92	July 14	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
93	28	8°45′	79°23′	37		x	x		obl.	x	x	0	x	x
94	Aug. 11	8°45′	79°23′	37	x	x	x		obl.			0	x	x
95	25	8°45′	79°23′	37		x	x	x	obl.	x	x	0	x	x
96	Sept. 8	8°45′	79°23′	37		x	x	x	obl.	x	x	0	x	x
97	22	8°45′	79°23′	37		x	x	x	obl.	x	x	0	x	x
98	Oct. 6	8°45′	79°23′	37		x	x	x	obl.			0	x	x
99	21	8°45′	79°23′	37		x	x	x	obl.	x	x			
100	Nov. 4	8°45′	79°23′	37		x	x	x	obl.	x	x	0	x	x
101	18	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
102	Dec. 2	8°45′	79°23′	37	x	x	x	x		x	x	0	x	x
	1959													
103	Jan. 2	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
104	13	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
105	28	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x

106	Mar. 6	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
107	19	8°45′	79°23′	37	x	x	x	x	obl.	x(5m)	x	0	x	x
108	Apr. 7	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
109	21	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
110	May 6	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
111	20	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x
112	June 3	8°45′	79°23′	37	x	x	x	x	obl.	x	x	0	x	x

*The samples used for the measurement of primary production were collected at the location indicated but were incubated at Taboga Island. Mr. Forsbergh did not believe these values are very reliable.

Table 8—AREA: NORTH EQUATORIAL, NORTH: INSHORE AND OFFSHORE

I.A.T.T.C. Progress Report. Physical, chemical and biological data, Costa Rica Dome Cruise, 6 Nov.-14 Dec., 1959. S.I.O. Ref. 60-20. April 1960.

												PHYTOPLANKTON						
				Hydro. Cast		Chemistry						Chlor. a		Productivity				
				Depth		Dis.	PO_4			Opt.			Water	Surface		Water Col.		
Sta. No.	Date 1959	Lat. N.	Long. W.	m	I.R.	O_2	-P	NO_2	NO_3	Meas.	Zoopl.	Surface	Col.	i.s.	li.	i.s.	li.
	Nov. 7	29°10′	116°22′		x									x			
	7	28°07′	116°04′		x							x		x			
	7	27°14′	114°48′									x					
	8	25°11′	114°05′		x			x	x					x			
	8	24°23′	113°20′		x			x	x					x			
	8	23°34′	112°34′					x	x			x					
	9	21°45′	110°57′		x			x	x			x		x			
	9	20°55′	110°21′		x			x	x			x		x			
	9	20°04′	109°36′					x	x			x					
	10	18°50′	107°36′		x			x	x					x			
	10	18°18′	106°45′		x			x	x					x			
	11	16°23′	103°50′		x			x	x					x			
A	11	16°05′	103°26′	1147				x	x						x		x
	11	16°00′	103°18′					x	x			x					
	11	15°25′	102°20′					x	x			x					
	12	14°38′	100°04′		x			x	x			x		x			
	12	14°17′	99°03′		x			x	x			x		x			
	12	13°56′	97°54′					x	x			x					
	13	13°02′	95°46′		x			x	x			x		x			
	13	12°40′	94°51′		x			x	x			x		x			
	13	12°17′	93°51′					x	x			x					
	14	11°27′	91°27′		x			x	x			x		x			
1	14	11°14′	91°16′	1097		x	x	x	x		c-B	x	x		x		x
	14	11°07′	91°16′		x							x		x			
	14	10°30′	90°36′									x					
	15	9°54′	89°40′		x							x		x			
	15	9°17′	89°14′		x							x		x			
7	15	9°00′	89°03′	1048		x	x	x	x		o,c-B	x	x		x		x
	15	8°58′	89°07′									x					
	16	7°59′	87°57′		x							x		x			
	16	7°34′	87°28′		x							x		x			

12		16	7°13′	87°11′	940		x	x	x	x		o	x	x		x		x
		17	8°12′	87°00′					x	x			x					
		17	9°20′	87°24′		x			x	x			x		x			
		17	10°25′	87°10′					x	x			x					
		18	8°35′	88°00′		x									x			
18		18	8°35′	88°00.5′	1150		x	x	x	x	K	s,o,c-B	x	x		x		x
		18	8°38′	88°12′									x					
		19	7°57′	89°48′		x									x			
22		19	7°39′	90°12′	1124		x	x	x	x	K	o	x	x		x		x
		19	7°17′	90°29′									x					
		20	7°17′	91°05′									x		x			
		20	8°09′	91°17′									x		x			
26		20	8°09′	91°17′	1150		x	x	x	x	K	s,o,c-B	x	x		x		x
		21	8°25′	89°47′		x							x		x			
		21	8°31′	89°29′									x		x			
30		21	8°10′	89°05′	1085		x	x	x	x		s,c-B	x	x		x		x
33		22	8°13′	87°52′	1090	x	x	x	x	x	K	s,o,c-B	x	x	x	x	x	x
		23	8°24′	86°29′		x							x		x			
36		23	8°52′	87°01′	1136		x	x	x	x	K	s,o	x	x		x		x
		27	9°20′	88°20′		x							x		x			
		27	9°37′	88°15′									x					
40		28	10°00′	88°20′	1135		x	x	x	x		s,o,c-B	x	x		x		x
		28	10°21′	88°25′		x							x		x			
		28	10°41′	88°20′		x							x		x			
		28	10°06′	89°01′									x					
		29	9°13′	90°09′		x							x		x			
43		29	9°13′	90°09′	1143		x	x	x	x		o	x	x		x		x
		29	9°00′	90°29′		x							x		x			
		29	8°52′	90°03′									x					
		30	8°33′	88°34′		x							x		x			
		30	8°13′	88°24′		x							x		x			
46		30	7°46′	88°26′	1097		x	x	x	x		s,o,c-B	x	x		x		x
	Dec.	1	7°13′	89°12′		x							x		x			
48		1	6°57′	88°49′	1144		x	x					x	x		x		x
49		2	6°25′	88°15′	1139		x	x					x	x				
50-7		3	5°35′	87°10′			x	x				s,o	x	x				
50-16		3	5°28′	86°58′			x	x				s,o	x	x				
		3	5°27′	86°57′		x							x		x			
		3	5°32′	87°01′		x							x		x			
		3	5°20′	87°05′									x					
53		4	5°29′	87°01′	110		x	x	x	x		c-B	x	x		x		x

Table 8—AREA: NORTH EQUATORIAL, NORTH: INSHORE AND OFFSHORE (Cont'd.)

I.A.T.T.C. Progress Report. Physical, chemical and biological data, Costa Rica Dome Cruise, 6 Nov.-14 Dec., 1959. S.I.O. Ref. 60-20. April 1960.

												PHYTOPLANKTON					
				Hydro. Cast		Chemistry						Chlor. a		Productivity			
				Depth		Dis.	PO_4			Opt.			Water	Surface		Water Col.	
Sta. No.	Date 1959	Lat. N.	Long. W.	m	I.R.	O_2	-P	NO_2	NO_3	Meas.	Zoopl.	Surface	Col.	i.s.	li.	i.s.	li.
56	4	5°35′	87°06′	200		x	x	x	x	K	o	x	x		x		x
	6	7°54′	88°22′									x		x			
	6	8°19′	88°47′									x		x			
	6	8°30′	89°12′									x					
	7	9°28′	91°25′									x		x			
	7	10°10′	92°33′		x							x		x			
	8	11°46′	95°50′		x							x		x			
	8	12°17′	96°52′		x							x		x			
	8	12°38′	97°56′									x					
	9	14°53′	101°39′									x					
	10	16°15′	104°33′									x					
	10	16°45′	105°34′									x		x			
	10	17°17′	106°33′									x					
	11	18°52′	108°38′									x		x			
	11	19°49′	109°17′		x							x		x			
	11	20°47′	109°57′									x					
	12	22°56′	111°26′		x							x		x			
	12	23°47′	112°04′		x							x		x			
	12	24°36′	112°47′														

Table 9 — AREA: NORTH AND SOUTH EQUATORIAL: NORTH: INSHORE AND OFFSHORE

I.A.T.T.C. Data report, STEP-I Expedition. Preliminary report. Part I. Physical and Chemical Data. Part II. Unpublished (E. Forsbergh). S.I.O. Ref. 61-9. 16 Jan. 1961.

Sta. No.	Date 1960	Lat.	Long. W.	Hydro. Cast Depth m	I.R.	Chemistry Dis. O_2	PO_4 -P	NO_2	Opt. Meas.	Nekton	Zoopl.	PHYTOPLANKTON Chlor. a. Surf.	Chlor. a. Water Col.	Productivity Surf. i.s.	Productivity Surf. di.	Productivity Water Col. i.s.	Productivity Water Col. di.
	Sept. 17	25°44′N	113°36′									x			x		
	17	25°05′	112°55′									x			x		
	18	23°34′	111°19′									x			x		
	18	22°54′	110°22′									x			x		
	18	22°20′	109°31′									x					
	19	21°03′	107°45′									x			x		
	19	20°26′	106°49′									x			x		
	19	19°45′	105°51′									x					
	20	18°03′	103°26′									x			x		
	20	17°42′	102°59′									x			x		
	20	17°10′	102°12′									x					
	21	15°59′	100°33′									x			x		
	21	15°25′	99°40′									x			x		
	21	14°40′	98°48′									x					
	22	13°22′	97°09′									x			x		
	22	12°41′	96°19′									x			x		
	22	12°03′	95°30′									x					
	23	10°41′	93°37′									x			x		
	23	10°05′	92°49′									x			x		
	23	9°30′	92°00′									x					
	24	8°12′	90°11′									x			x		
	24	7°30′	89°19′									x			x		
	24	6°45′	88°22′									x					
	25	5°16′	86°50′									x			x		
	25	4°08′	86°20′									x			x		
	25	3°22′	86°06′									x					
	26	1°41′	85°36′									x			x		
	26	0°44′	85°18′									x			x		
	26	0°02′	85°03′									x					
	27	0°10′S	84°59′									x			x		
	27	0°58′	84°40′									x			x		

Table 9—AREA: NORTH AND SOUTH EQUATORIAL: NORTH: INSHORE AND OFFSHORE (Cont'd.)

												PHYTOPLANKTON					
				Hydro. Cast		Chemistry						Chlor. a.		Productivity			
				Depth		Dis.	PO_4		Opt.				Water	Surf.		Water Col.	
Sta. No.	Date 1960	Lat.	Long. W.	m	I.R.	O_2	-P	NO_2	Meas.	Nekton	Zoopl.	Surf.	Col.	i.s.	di.	i.s.	di.
	27	1°48′	84°21′									x					
1	28	2°06′	84°14′	1172	x	x	x	x	K	obl.	s,o,c-B	x	x			x	
	29	1°34′	83°10′									x			x		
	29	1°08′	82°20′									x			x		
	30	1°00′	82°05′									x			x		
	30	1°41′	82°20′									x			x		
	30	2°28′	82°20′									x					
3	Oct. 1	1°50′	81°41′	1222	x	x	x	x	K	obl.	s,o,c-B	x	x			x	
	1	1°50′	81°41′												x		x
4	1 & 2	2°13′	82°00′	1278	x	x	x	x	K	obl.	s,o,c-B	x	x			x	
	2	2°13′	82°00′										x			x	x
	2	2°30′	81°30′									x					
4C	3	2°57′	80°55′	183		x	x	x				x			x		
	3	3°21′	80°50′									x			x		
	3	3°58′	81°44′									x					
	4	3°06′	82°23′									x			x		
	4	2°52′	81°43′									x			x		
	4	3°28′	81°54′									x					
	6	5°42′	81°19′									x			x		
	6	6°02′	81°18′									x					
	7	6°02′	81°18′									x			x		
4E	7	6°02′	81°18′		x				K			x	x		x	x	x
5	8	6°02′	81°18′	1248		x	x	x			o,c-B	x			x		
	8	6°05′	81°28′									x			x		
6	8	6°23′	81°54′	1265		x	x	x		obl.	s,o,c-B	x					
7	9	6°43′	82°27′	1251		x	x	x			c-B	x			x		
8	9	7°02′	82°56′	1254	x	x	x	x	K		o	x	x		x	x	
	9	7°16′	83°20′									x					
10	10	8°02′	84°45′	1242	x	x	x	x	K		o	x	x		x		x
	11	9°09′	86°36′												x		
	11	9°09′	86°36′									x			x		
	11	9°55′	87°54′									x					

13		12	10°35′	89°06′	1195		x	x	x			s,o,c-B	x		x		
		12	11°04′	89°59′									x		x		
14		12	11°26′	90°34′	1158		x	x	x			c-B	x				
		13	12°41′	89°54′									x		x		
15		13	13°18′	89°35′	1124	x	x	x	x	K		o	x	x	x		x
		14	15°02′	88°24′									x		x		
16		14	15°40′	87°58′	1219	x	x	x	x	K		o,c-B	x	x	x		x
17		15	14°49′	86°26′	1243		x	x	x		obl.	s,o	x				
		15	14°16′	85°28′									x				
		15	13°54′	84°45′									x				
19		16	13°11′	83°32′	1246		x	x	x		obl.	s,o,c-B	x		x		
		16	13°03′	83°12′										x	x		x
20		16	12°26′	82°08′	1206		x	x	x			c-B	x				
21		17	11°51′	81°12′	1280		x	x	x			c-B	x		x		
22		17	11°27′	80°32′	1282		x	x	x			c-B	x		x		
23		17	11°10′	80°01′	1134		x	x	x		obl.	s,o,c-B	x				
		18	10°49′	79°24′									x		x		
25		18	10°32′	78°52′	788		x	x	x	K		o	x	x	x		x
25A		19	10°32′	78°52′						K			x			x	
		20											x		x		
	Oct.	26	11°57′	77°44′									x		x		
		26	12°20′	77°31′									x				
		27	13°45′	76°42′									x		x		
		27	13°45′	76°42′										x	x	x	x
		28	14°27′	76°24′									x		x		
26		28	14°51′	76°09′	949		x	x	x			c-B	x				
		29	15°22′	76°55′									x		x		
28		29	15°40′	77°20′	1159	x	x	x	x	K		s,o	x	x	x		x
30		30	16°27′	78°38′	1200		x	x	x		obl.	s,o,c-B	x		x		
		30	17°06′	79°20′									x		x		
		30	17°28′	80°00′									x				
32		31	18°06′	80°56′	1213		x	x	x		obl.	s,o,c-B	x		x		
		31	18°41′	81°43′									x		x		
33		31	19°04′	82°18′	1206		x	x	x			c-B	x				
34	Nov.	1	20°05′	83°42′	1272		x	x	x			c-B	x		x		
34A		1	20°26′	84°11′		x				K		o	x	x	x		x
35		1	20°55′	85°16′	1194		x	x	x		obl.	s,o	x				
		2	21°38′	84°08′									x		x		
		2	22°11′	83°18′									x		x		
		2	22°37′	82°47′									x				
		3	23°41′	81°13′									x		x		

Table 9 — AREA: NORTH AND SOUTH EQUATORIAL: NORTH: INSHORE AND OFFSHORE (Cont'd.)

												PHYTOPLANKTON					
						Chemistry						Chlor. a.		Productivity			
				Hydro. Cast Depth		Dis.	PO_4		Opt.				Water	Surf.		Water Col.	
Sta. No.	Date 1960	Lat.	Long. W.	m	I.R.	O_2	-P	NO_2	Meas.	Nekton	Zoopl.	Surf.	Col.	i.s.	di.	i.s.	di.
37	3	23°45′	81°07′	1262	x	x	x	x	K		o,c-B	x	x		x		x
	3	23°16′	80°27′									x	x				
	4	22°27′	79°21′									x	x		x		
	4	21°37′	78°28′									x			x		
	5	20°29′	76°39′									x			x		
	5	19°38′	75°32′									x			x		
43	6	18°18′	74°03′	1204		x	x	x			c-B	x			x		
	6	17°53′	73°31′									x			x		
46	7	17°12′	72°19′	972		x	x	x			c-B	x			x		
46A	7	17°03′	72°15′		x				K			x	x		x	x	x
	8	17°03′	72°15′									x			x		
	10	17°59′	72°02′									x			x		
	10	19°03′	71°58′									x			x		
47	10	19°09′	71°58′	2108		x	x	x			c-B	x					
	11	20°53′	71°17′									x			x		
48	11	21°16′	71°09′	2134		x	x	x			o	x			x		
	11	21°57′	71°08′									x					
48A	12	23°31′	70°53′		x				K			x	x		x	x	x
	13	23°31′	70°53′									x			x		
	13	23°31′	70°53′									x			x		x
49	17	23°40′	70°38′		x				K		c-B	x	x		x		x
51	18	23°48′	72°00′	1189		x	x	x			c-B	x			x		
52	18	23°54′	72°37′	1272		x	x	x			c-B	x			x		
	18	23°46′	73°18′									x					
	19	23°41′	74°44′									x			x		
54A	19	23°42′	75°03′		x				K		o	x	x		x		x
56	20	23°38′	77°06′	1291		x	x	x			o	x			x		
	20	23°38′	77°49′									x			x		
57	20	23°39′	78°55′	1358		x	x	x			c-B	x					
	21	23°41′	80°29′									x			x		
58	21	23°41′	80°42′	1340	x	x	x	x	K		o	x	x		x		x
	22	23°43′	83°12′									x			x		
	22	23°43′	83°02′									x			x		
	22	23°42′	85°04′									x					

61		23	23°41′	86°09′	1244		x	x	x			c-B	x			x	
		23	23°40′	87°13′									x			x	
		23	23°41′	88°01′									x				
63		24	23°41′	89°37′	1241		x	x	x			c-B	x			x	
63A		24	23°41′	90°06′		x				K			x	x		x	x
65		25	23°41′	93°11′	1176		x	x	x			c-B	x			x	
		25	23°40′	94°50′									x				
		26	23°18′	95°14′									x			x	
		26	22°10′	95°09′									x			x	
		26	21°30′	95°07′									x				
68		27	19°55′	95°05′	1259		x	x	x			o	x	x		x	
68A		27	19°32′	95°05′		x				K			x			x	x
69		27	18°16′	95°05′	1158		x	x	x		obl.	s,o,c-B	x				
		28	16°50′	94°09′												x	
		28	16°02′	94°56′									x			x	
71		28	15°03′	95°04′	1223		x	x	x			c-B	x				
		29	13°33′	94°58′									x			x	
72A		29	13°04′	94°56′		x				K			x	x		x	x
		29	11°41′	94°59′									x				
		30	10°18′	95°01′									x			x	
		30	9°44′	94°59′									x			x	
		30	8°34′	94°56′									x				
	Dec.	1	6°55′	94°52′									x			x	
76A		1	6°34′	94°52′		x				K			x	x		x	x
		1	5°13′	94°59′									x				
		2	4°10′	95°05′									x			x	
		2	3°25′	95°02′									x			x	
		2	2°35′	94°56′									x				
81		3	0°58′	94°54′	1275		x	x	x			c-B	x			x	
81A		3	0°40′	94°54′		x				K			x	x		x	x
83		4	1°08′N	95°10′	1015		x	x	x			c-B	x			x	
84		4	1°59′	95°02′	1205		x	x	x			o	x			x	
		4	2°43′	95°02′									x				
		5	4°02′	94°56′									x		x	x	
86		5	4°02′	94°56′	1258		x	x	x			o		x		x	x
		6	6°56′	95°01′									x			x	
		6	7°56′	95°01′									x			x	
		6	8°41′	95°01′									x				
90		7	10°05′	95°06′	1276		x	x	x			o	x			x	
		7	10°46′	95°48′									x			x	
		7	11°26′	96°47′									x				
		8	13°00′	98°41′												x	

Table 9—AREA: NORTH AND SOUTH EQUATORIAL: NORTH: INSHORE AND OFFSHORE (Cont'd.)

Sta. No.	Date 1960	Lat.	Long. W.	Hydro. Cast Depth m	I.R.	Chemistry: Dis. O_2	Chemistry: PO_4 -P	Chemistry: NO_2	Opt. Meas.	Nekton	Zoopl.	PHYTOPLANKTON Chlor. a. Surf.	PHYTOPLANKTON Chlor. a. Water Col.	PHYTOPLANKTON Productivity Surf. i.s.	PHYTOPLANKTON Productivity Surf. di.	PHYTOPLANKTON Productivity Water Col. i.s.	PHYTOPLANKTON Productivity Water Col. di.
	8	13°49′	99°39′									x			x		
	8	14°23′	100°25′									x					
	9	15°46′	102°05′									x			x		
	9	16°25′	102°49′									x			x		
	9	17°02′	103°34′									x					
	10	18°33′	105°23′									x			x		
	10	19°14′	106°13′									x			x		
	10	19°52′	106°57′									x					
	11	21°22′	108°43′									x			x		
	11	22°07′	109°36′									x			x		
	11	22°47′	110°01′									x					
	12	24°19′	112°05′									x			x		
	12	24°55′	113°04′									x			x		

Table 10—AREA: NORTH AND NORTH EQUATORIAL: INSHORE AND OFFSHORE

Koblens-Mishke, O. J. Study of primary production of the sea by Soviet scientists. Vityaz Cruise No. 29, biological data (plankton). Productivity for stations in the eastern Pacific.

Sta. No.	Date 1958	Lat. N.	Long. W.	Hydro. Cast Depth m	Chemistry: Dis. O_2	Chemistry: PO_4 -P	Chemistry: NO_2	Chemistry: NO_3	Chemistry: pH	Chemistry: Alk.	Chemistry: Si	Chemistry: CO_2	Nekton*	Zoopl.*	Productivity Surface i.s.	Productivity Surface di.	Productivity Water Col. i.s.	Productivity Water Col. di.
4171	Dec. 1	44°57′	131°05′	2800	x	x	x		x	x	x	x				x		x
4173	2	44°58′	128°51′	2670	x	x	x	x	x	x	x	x	I-K	V(J-1)		x		x
4177	4	44°51′	125°04′	687	x	x	x	x	x	x	x	x		V(J-8)		x		x
4181	5	40°00′	125°08′	1500	x	x	x	x	x	x	x	x	S	V(J-7)		x		x
4183	6	40°01′	127°39′	2062	x	x	x	x	x	x	x	x	I-K	V(J-7)		x		x
4187	7	40°03′	131°26′	2193	x	x	x		x	x	x	x	S	V(J-7)		x		x

4191	8	40°20′	135°46′	3977	x	x	x	x	x	x	x	x	S	V(J08)	x	x	x	x
4217	26	29°58′	120°43′	4045	x	x	x	x	x	x	x	x	I-K	V(J-7)	x	x	x	x
4219	27	30°00′	123°14′	2242	x	x	x		x	x	x	x		V(J-6)		x		x
4223	28	29°59′	128°34′	2234	x	x	x		x	x	x	x		V(J-6)		x		x
4229	30	30°03′	136°29′	2502	x	x	x	x	x	x	x	x		V(J-1)		x		x
4233	31	30°00′	141°40′	1801	x	x	x		x	x	x	x				x		x
	1959																	
4237	Jan. 1	27°24′	144°02′	2417	x	x	x		x	x	x	x		V(J-7)		x		x
4239	3	24°53′	143°54′	5000	x	x	x	x	x	x	x	x	S,I-K,SI	V(J-8)		x		x
4243	4	25°00′	139°42′	2181	x	x	x		x	x	x	x	S	V(J-11)	x	x	x	x
4245	5	24°59′	137°19′	2281	x	x	x	x	x	x	x	x		V(J-7)		x		x
4249	7	24°55′	132°17′	4785	x	x	x	x	x	x	x	x	S,I-K	V(J-6)	x	x		x
4251	8	25°00′	129°57′	2025	x	x	x		x	x	x	x		V(J-6)		x		x
4255	9	25°02′	125°10′	2137	x	x	x		x	x	x	x	S	V(J-7)		x		x
4259	10	24°56′	120°10′	2145	x	x	x		x	x	x	x	S	V(J-6)		x		x
4261	11	24°57′	117°50′	3505	x	x	x	x	x	x	x	x	S,I-K	V(J-7)		x		x
4265	13	24°58′	113°25′	2137	x	x	x	x	x	x	x	x	S	V(J-6,C-1)		x		x
4266	14	23°12′	111°57′											V(J-6)		x		x
4268	15	19°59′	109°03′	2011	x	x	x		x	x	x	x	S	V(J-7)		x		x
4269	16	20°00′	110°02′	2868	x	x	x	x	x	x	x	x	S,I-K	V(J-7)		x		x
4271	17	20°00′	111°57′	2072	x	x	x	x	x	x	x	x	S	V(J-7)		x		x
4275	19	20°04′	115°51′	2193	x	x	x		x	x	x	x	S	V(J-7)		x		x
4279	19	19°50′	120°15′	4035	x	x	x	x	x	x	x	x	S,I-K,R	V(J-7)		x		x
4281	21	20°01′	121°59′	2210	x	x	x		x	x	x	x	S	V(J-7)		x		x
4285	22	20°00′	126°02′	2223	x	x	x	x	x	x	x	x	S	V(J-6)		x		x
4289	23	20°00′	130°01′	4966	x	x	x	x	x	x	x	x	S,I-K	V(J-7)		x		x
4295	26	19°58′	136°01′	3011	x	x	x		x	x	x	x	S,I-K			x		x
4301	27	20°10′	142°04′	2371	x	x	x	x	x	x	x	x	S	V(J-1)		x		x
4307	29	20°02′	147°58′	2107	x	x	x		x	x	x	x	S	V(J-1)		x		x
4309	30	20°04′	150°00′	4522	x	x	x	x	x	x	x	x	S,I-K	V(J-6)		x		x
4311	31	20°03′	151°48′	4864	x	x	x		x	x	x	x	S	V(J-7)		x		x
4313	Feb. 1	20°00′	154°05′	2371	x	x	x		x	x	x	x	S,SI			x		x

*V = Vertical
J = Juday Net
S = Surface Trawl
SI = Sigsby Trawl
I-K = Isaak-Kidd Trawl
C = Conical Net
R = Ring Trawl

NOTE: The data which served as the basis for this compilation was obtained from the World Data Center A. Incident solar radiation records and vertical attenuation coefficient (k) data are apparently available, although they were not included in data sheets available at the W.D.C. Identification and abundance estimates of phytoplankton have been made at vitually every station listed above.

Table 11 — AREA: NORTH: INSHORE AND OFFSHORE

Love, C. M. and G. C. Anderson. Preliminary Report: Brown Bear Cruise 275. Coastal and Offshore Survey 10-27 January, 1961.

										PHYTOPLANKTON													
										Chlorophylls								Productivity					
										Surface			Water Col.					Surface		Water Col.		Water Sample for Spec. Ident.
Sta. No.	Date 1961	Lat. N.	Long. W.	Hydro. Cast Depth m	I. R.	PO_4 -P	NO_3 -N	Opt. Meas.	Zoopl.	a	b	c	a	b	c	NAC	AC	li.	di.	li.	di.	
1	Jan. 10-11	48°17′	124°03′	174	x					x	x	x	x	x	x	x	x	x		x		
10A	12									x	x	x				x	x	x				x
11	16	46°12′	129°39′	1639	x	x	x			x	x	x	x	x	x	x	x	x	x	x		x
12	17	45°03′	127°07′	1713	x	x	x			x	x	x	x	x	x	x	x	x		x		x
13	18	44°23′	125°54′	2184	x					x	x	x	x	x	x	x	x	x		x		x
14	18	44°12′	125°25′	2152		x	x	K		x	x	x	x	x	x	x	x	x		x		x
15	18	44°07′	124°43′	90	x					x	x	x	x	x	x	x	x	x		x		x
16	18-19	44°03′	124°25′	100					c-B	x	x	x	x	x	x	x	x	x		x		x
17	19	44°00′	124°11′	33	x					x	x	x	x	x	x	x	x	x		x		x
17D	19									x	x	x				x	x	x				
18	19	44°18′	124°10′	40						x	x	x	x	x	x	x	x	x		x		x
19	19			45		x	x															
20	19	44°38′	124°18′	78					c-B	x	x	x	x	x	x	x	x	x		x		x
21	19	44°46′	124°40′	200						x	x	x	x	x	x	x	x	x		x		x
22	19-20	45°02′	125°20′	1864	x				c-B	x	x	x	x	x	x	x	x	x		x		x
23	20	45°10′	124°56′	705						x	x	x	x	x	x	x	x	x		x		x
24	20	45°21′	124°29′	390		x	x		c-B	x	x	x	x	x	x	x	x	x		x		x
25	20	45°26′	124°12′	117						x	x	x	x	x	x	x	x	x		x		
25A	20	45°28′	124°08′																			x
26	20	45°32′	124°01′	29						x	x	x	x	x	x	x	x	x		x		x
27	20	45°37′	124°09′	96						x	x	x	x	x	x	x	x	x		x		x
28	21	45°48′	124°38′	123	x				c-B	x	x	x	x	x	x	x	x	x		x		x
29	21	45°40′	125°01′	1475						x	x	x	x	x	x	x	x	x				
29D	21									x	x	x				x	x	x				
30	21	45°31′	125°21′	1779					c-B	x	x	x	x	x	x	x	x	x		x		
31	21	45°41′	125°30′	1953						x	x	x	x	x	x	x	x	x		x		x
32	21	45°52′	125°33′	1259		x	x			x	x	x	x	x	x	x	x	x		x		x
33	22	45°58′	125°21′	1205	x				c-B	x	x	x	x	x	x	x	x	x		x		
34	22	46°06′	125°04′	1229						x	x	x	x	x	x	x	x	x		x		

35	22	46°12′	124°47′	633		x	x	c-B	x	x	x	x	x	x	x	x	x	x	x		x
36	22	46°17′	124°33′	123					x	x	x	x	x	x	x	x	x		x		x
37	22	46°21′	124°24′	70					x	x	x	x	x	x	x	x	x		x		x
38	22	46°25′	124°11′	32		x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
39	22	46°10′	124°11′	35		x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
40	22	46°02′	124°06′	59					x	x	x	x	x	x	x	x	x		x		x
41	23	45°52′	124°00′	29	x			c-B	x	x	x	x	x	x	x	x	x	x	x	x	x
42	23	45°52′	124°13′	49					x	x	x	x	x	x	x	x	x		x		x
43	23	46°05′	124°13′	120					x	x	x	x	x	x	x	x	x		x		x
44	23	46°26′	125°21′	1961				c-B	x	x	x	x	x	x	x	x	x		x		x
45	23	46°36′	125°40′	1897		x	x		x	x	x	x	x	x	x	x	x		x		x
46	23-24	46°39′	125°09′	927				c-B	x	x	x	x	x	x	x	x	x		x		
47	24	46°44′	124°48′	193	x				x	x	x	x	x	x	x	x	x		x		x
47D	24								x	x	x				x	x	x				
48	24	46°47′	124°27′	68					x	x	x	x	x	x	x	x	x		x		
49	24	46°50′	124°13′	29					x	x	x	x	x	x	x	x	x		x		x
49A	24																				x
50	24	46°57′	124°18′	29				c-B	x	x	x	x	x	x	x	x	x		x		x
51	24	47°12′	124°22′	29		x	x		x	x	x	x	x	x	x	x	x		x		
52	24	47°11′	124°36′	59					x	x	x	x	x	x	x	x	x		x		x
53	24	47°10′	124°56′	166					x	x	x	x	x	x	x	x	x		x		x
54	24-25	47°13′	125°20′	1162				c-B	x	x	x	x	x	x	x	x	x		x		
55	25	47°17′	126°10′	1953	x	x	x		x	x	x	x	x	x	x	x	x		x		x
55A	25							c-B	x	x	x	x	x	x	x	x	x		x		
56	25	47°34′	126°02′	997					x	x	x	x	x	x	x	x	x		x		
57	25	47°52′	125°56′	1366					x	x	x	x	x	x	x	x	x		x		x
58	25-26	47°43′	125°33′	923		x	x	c-B	x	x	x	x	x	x	x	x	x		x		
59	26	47°39′	125°20′	720	x				x	x	x	x	x	x	x	x	x		x		x
59D	26								x	x	x				x	x	x				
60	26	47°31′	125°02′	341					x	x	x	x	x	x	x	x	x		x		
61	26	47°24′	124°42′	98				c-B	x	x	x	x	x	x	x	x	x		x		x
62	26	47°42′	124°37′	30		x	x		x	x	x	x	x	x	x	x	x		x		x
63	26	47°49′	124°49′	64					x	x	x	x	x	x	x	x	x		x		x
64	26	47°58′	125°03′	114					x	x	x	x	x	x	x	x	x		x		
65	26	48°08′	125°14′	228		x	x		x	x	x	x	x	x	x	x	x		x		x
66	26-27	48°17′	125°03′	167				c-B	x	x	x	x	x	x	x	x	x		x		x
67	27	48°27′	124°47′	156	x	x	x		x	x	x	x	x	x	x	x	x		x		x

Similar observations likewise obtained on Brown Bear Cruise 280 et seq. Complete information not yet available.

Table 12—AREA: NORTH AND NORTH EQUATORIAL: INSHORE AND OFFSHORE

Steemann Nielsen, E. and E. Asbye Jensen. Primary Oceanic Production. The autotrophic production of organic matter in the oceans. Galathea Report I: 49-136.

Sta. No.	Date 1952	Lat. N.	Long. W.	Temp. °C	PO_4 -P	PS Layer Depth m	PHYTOPLANKTON Chlorophylls	Productivity Surface li.	Productivity Water Col. li.
698	Mar. 29	23°00′	155°25′	x	x	105		x	x
698a	31	26°52′	148°32′			100		x	x
699	Apr. 3	33°37′	134°53′	x	x	97		x	x
700	4	35°45′	129°10′	x	x	77		x	x
701	5	37°16′	124°36′	x	x	63		x	x
705	22	32°50′	117°32′	x	x	23		x	x
707	24	26°00′	113°31′	x	x	67		x	x
708	25	22°50′	110°06′	x	x	34		x	x
709	26	20°00′	106°12′	x	x	55		x	x
715	May 4	13°00′	95°48′	x	x	80		x	x
717	7	8°41′	86°12′	x	x	52		x	x
719a	10	6°52′	79°30′			60		x	x
720	11	5°36′	79°31′	x	x	60		x	x
723	12	6°00′	79°54′			60		x	x

Table A—NORTHERN REGION (N of 25° N)

S.I.O. and I.A.T.C.

	Number of Observations: in situ Surface	in situ Water Column	Laboratory Incubator Surface	Laboratory Incubator Water Column
Inshore	4	2	7	3
Offshore	1	-	2	-

Median Productivity and Range of Values

	in situ Surface $mgC/m^3/day$ Lowest	Median	Highest	in situ Water Column $mgC/m^2/day$ Lowest	Median	Highest	Laboratory Incubator Surface $mgC/m^3/day$ Lowest	Median	Highest	Laboratory Incubator Water Column $mgC/m^2/day$ Lowest	Median	Highest
Inshore	0.48	0.742	2.60	0.153	-	33.6	0.098	0.306	8.821	1.8	5.0	21.9
Offshore	-	1.84	-	-	-	-	0.048	-	1.069	-	-	-

Table B—NORTH EQUATORIAL PACIFIC (0-25° N)

S.I.O. and I.A.T.C.

	Number of Observations: in situ Surface	in situ Water Column	Laboratory Incubator Surface	Laboratory Incubator Water Column
Inshore	32	10	39	16
Offshore	132	13	92	9

Median Productivity and Range of Values

	in situ Surface $mgC/m^3/day$ Lowest	Median	Highest	in situ Water Column $mgC/m^2/day$ Lowest	Median	Highest	Laboratory Incubator Surface $mgC/m^3/day$ Lowest	Median	Highest	Laboratory Incubator Water Column $mgC/m^2/day$ Lowest	Median	Highest
Inshore	0.605	5.5	140	0.185	100	952	0.0345	0.858	16.0	8.0	28.8	830
Offshore	0.13	6.1	414	0.012	0.442	400	0.015	0.47	10.4	5.0	20.7	116

Table C—SOUTH EQUATORIAL PACIFIC (0-25° S)

S.I.O. and I.A.T.T.C.

	Number of Observations			
	in situ		Deck Incubator	
	Surface	Water Column	Surface	Water Column
Inshore	36	8	34	8
Offshore	61	1	62	15

	Median Productivity and Range of Values											
	in situ						Deck Incubator					
	Surface mgC/m³/day			Water Column mgC/m²/day			Surface mgC/m³/day			Water Column mgC/m²/day		
	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest
Inshore	1.9	13	190	70	120	280	3.2	20	200	50	150	320
Offshore	0.0	2.0	41	-	10	-	0.0	3.7	45	35	80	240

Table D—GALATHEA REPORT (PACIFIC OCEAN)

(Laboratory incubator only)

	North Equatorial (0-25° N)		Northern Region (N of 25° N)	
	Number of Observations		Number of Observations	
	Surface	Water Column	Surface	Water Column
Inshore	2	2	2	2
Offshore	6	6	4	4

	North Equatorial: Median Productivity and Range of Values						Northern Region: Median Productivity and Range of Values					
	Surface mgC/m³/day			Water column mgC/m²/day			Surface mgC/m³/day			Water column mgC/m²/day		
	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest
Inshore	0.59	-	3.5	0.21	-	0.9	0.59	-	2.1	0.24	-	0.36
Offshore	0.31	0.73	1.9	0.19	0.27	0.48	0.08	0.11	0.89	0.08*	0.1	0.55

* Approx.

Table E—P.O.F.I. AND UNIVERSITY OF HAWAII

(Laboratory Incubator only)

	South Equatorial Pacific 0-25° S	North Equatorial 0-25° N	Northern Region N of 25° N
	Number of Observations	Number of Observations	Number of Observations
Inshore	-	2	5
Offshore	42	61	65

	Median Productivity and Range of Values — Surface Samples only (mgC/m³/hr.)								
	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest
Inshore	-	-	-	0.59	-	24.00	0.228	0.797	1.854
Offshore	0.033	0.12	18.0	0.014	0.332	17.35	0.016	0.107	3.672

Table F—VITYAZ CRUISE 29

North Equatorial (0-25° N)

	Number of Observations: in situ Surface	in situ Water Column	Deck Incubator Surface	Deck Incubator Water Column
Inshore	-	-	2	-
Offshore	2	1	19	-

Median Productivity and Range of Values

	in situ Surface $mgC/m^3/day$			in situ Water Column $mgC/m^2/day$			Deck Incubator Surface $mgC/m^3/day$			Deck Incubator Water Column $mgC/m^2/day$		
	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest
Inshore	-	-	-	-	-	-	<0.1	-	2.2	-	-	-
Offshore	1.0	-	3.5	-	350.0	-	<0.1	0.2	7.8	-	-	-

Table G—VITYAZ CRUISE 29

Northern Region (N of 25° N)

	Number of Observations: in situ Surface	in situ Water Column	Deck Incubator Surface	Deck Incubator Water Column
Inshore	1	1*	1	-
Offshore	2	2	10	-

Median Productivity and Range of Values

	in situ Surface $mgC/m^3/day$			in situ Water Column $mgC/m^2/day$			Deck incubator Surface $mgC/m^3/day$			Deck incubator Water Column $mgC/m^2/day$		
	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest	Lowest	Median	Highest
Inshore	-	26.0	-	-	203.0*	-	-	<0.1	-	-	-	-
Offshore	1.2	-	2.0	7.04	-	254.1	<0.1	2.8	5.5	-	-	-

*Calculated

Table H—NORTH EQUATORIAL PACIFIC

Gulf of Panama, 8°45′ N 79°23′ W

Inter-American Tropical Tuna Commission

	Number of Observations	
	Surface	Water Column
January	12	3
February	6	0
March	7	2
April	8	3
May	6	3
June	7	4
July	7	2
August	6	2
September	5	2
October	6	1
November	5	2
December	6	1

Median Productivity and Range of Values*

	Surface mgC/m^3/day			Water Column mgC/m^2/day†		
	Lowest	Median	Highest	Lowest	Median	Highest
January	9.2	17.0	180.0	0.160	0.263	0.725
February	9.2	38.0	42.0	-	-	-
March	1.5	26.0	81.0	0.528		1.295
April	4.7	31.0	110.0	0.465	0.765	1.270
May	6.9	43.0	74.0	0.540	0.562	0.575
June	3.1	10.0	83.0	0.160	0.185	0.530
July	3.4	12.0	30.0	0.233	-	0.243
August	3.0	10.0	40.0	0.278	-	0.415
September	1.3	6.3	19.0	0.170	-	0.230
October	1.2	12.0	79.0	-	0.303	-
November	1.9	19.0	25.0	0.193	-	0.328
December	4.6	9.4	31.0	-	0.335	-

*Both surface and 10-meter values have been utilized in this compilation.
†Samples were incubated for 24 hours adjacent to Tabaga Is.

OUR KNOWLEDGE OF THE KINDS OF ORGANISMS IN PACIFIC PHYTOPLANKTON

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INTRODUCTION

The results of existing studies on the phytoplankton of various areas of the Pacific Ocean are given in Tables 1-13. The works on which these tables are based vary greatly in their scope, some being detailed records of a limited region over a period of years, such as the studies of W. E. Allen in Southern California (Table 1), Phifer in the Puget Sound area (Table 2), and Wood in Australia (Table 11), while others are the result of a single cruise. The data collected by the *Vityaz* during a cruise from October 1958 through February 1959 covering most of the Eastern Pacific Ocean north of 19° N have been presented in some detail because of the broad synoptic picture of phytoplankton distributon that they reveal.

With a few exceptions, which will be discussed below, these studies are based on collections made with plankton nets, and the material has usually been examined after preservation. This has the consequence that the organisms studied are principally the diatoms and those dinoflagellates which are not unduly distorted by preservation. For these groups, it will be seen that at least some information is available for a large part of the Pacific Ocean.

Cosmopolitan and Indicator Forms

Two types of organisms represented in these studies appear to deserve special attention. The first is of the cosmopolitan oceanic forms that appear to be able to develop over a wide range of temperatures, salinities, and nutrient conditions. Examples of these are *Thalassiothrix longissima*, *Rhizosolenia alata*, *Chaetoceros atlanticus*, and *Ceratium tripos*. Perusal of the tables will reveal others. Such organisms constitute prime targets for cultural studies on oceanic phytoplankton.

The second group of special interest is those organisms which, by contrast, occur only under a limited range of hydrographic conditions and thus serve as indicators for water masses. A notable example is *Rhizosolenia curvata*, which occurs (Hart, 1937) only around the Antarctic Convergence. Wood (1954) pointed out several diatoms and Crosby and Wood (1958) have dinoflagellates characteristic of various water masses near Australia, as shown in Table 11.

The data in Table 5 indicate the complexity of the population encountered, especially in warmer waters, where the typical situation is for many species to co-exist without any one becoming dominant (cf. also Steemann-Nielsen, 1934; Hasle, 1959). Since most of the organisms are known only from preserved collections and have not been studied experimentally, it is possible that the number of species may be somewhat reduced when the range of variation of each is known.

In this compilation, the names and classifications of the organisms are those used by the authors of the original reports. It is recognized that this results in some conflict of nomen-

clature, but to deal adequately with the taxonomic problems involved is beyond the scope of this paper and the competence of its author. Certain other differences between reports will also become evident on studying the tables. For example, Rhizosolenia alata and Chaetoceros atlanticus, which are listed as cold water forms in Table 7, were found in the equatorial Pacific by Hasle (1959).

Nannoplankton

In contrast to the relatively abundant information on diatoms and dinoflagellates is the extreme paucity of data on the smaller phytoplankters. The studies of Hasle (1959) and of Norris (1961a) give some information for the tropical Pacific, while Norris (1961b) and Scagel and Stein (1961) have examined Wellington Harbor, New Zealand, and a British Columbia fjord. (It is worthy of note that several of the same species occurred in these widely separated estuaries, and that the microflora of both includes forms described by Butcher (1952) from the British coast.) This, except for general statements, e.g., "coccolithophorids present" is the extent of our knowledge of the Pacific nannoplankton.

For some regions, at least, this lack of knowledge of the smaller phytoplankters is a serious gap in information about the organisms responsible for primary production. Studies in other oceans (Steemann-Nielsen, 1938; Steemann-Nielsen and Jensen, 1957; Riley, 1941a; Harvey, 1950; Wood and Davis, 1956; Yentsch and Ryther, 1959) have shown the nannoplankton to be an important part of the microflora. Wood (1961) has estimated that the ratio of nannoplankton to net phytoplankton in the Tasman Sea is of the order of 100/1, while in the Coral Sea almost all production was found to be due to nannoplankton. In some waters, however, the larger plankters are considered to predominate.

Investigation of the nannoplankton thus appears to be the most urgent problem facing students of the primary producing organisms. A successful attack on this problem will require a considerable departure from standard methods of phytoplankton study. First, as already has been mentioned, many of the organisms must be observed in the living state. This means (a) that the student of the nannoplankton must go to sea, and (b) that the collections must be made in such a way as to obtain healthy living material. Except in rich estuarine environments, in order to obtain a significant picture of the population, large water volumes must be collected and the organisms in them concentrated. The apparatus used for collecting should be of such design that the organisms do not come into contact with toxic metals. Since a number of designs for non-metallic water samplers exist, this aspect of the problem does not appear to pose serious obstacles. Concentration without damage to cells, however, requires more study. Since many of the organisms are small and motile, simple settling, as is used with preserved samples, cannot be relied upon, and either centrifugation or filtration must be used. Both are hazardous because of the mechanical fragility of many of the cells. Filtration through Millipore filters is readily carried out in the field, and methods for quantitative transfer of the organisms collected to culture media are known. However, the results of Holmes (1961a), in which an appreciable portion of carbon-14 fixed by phytoplankton passed through a filter with a pore size of 0.45 μ, suggest that fragmentation of cells may occur during filtration. Mechanical damage to cells can be minimized by the use of filters of large size under a low pressure and the exclusion of air bubbles from the system, but further quantitative studies in this area are badly needed.

Identification of the organisms collected is the next problem, and one which is much more serious because of the shortage of experts who can deal with it. This work would be greatly facilitated if a handbook or guide to the identification of phytoplankton, at least to the generic level, could be prepared. The present literature is scattered and often not readily accessible.

Since identification of some nannoplankters requires electron microscopy, preparation of cultures for this and for other detailed investigation is an important part of any study of these organisms. This approach was advocated several years ago by Knight-Jones (1951). Oceanic phytoplankton has not so far been very amenable to culture, but it appears likely that at least some of the difficulty can be ascribed to the constant conditions under which the oceanic forms live, compared to the shocks and changes to which they are subjected on being taken back to the laboratory for cultivation. Starting of cultures immediately after collection, together with

concentration of samples and their incubation under constant temperature conditions comparable to those found in the sea from which they were collected, would appear to be indispensable requirements. The latter will probably be easier to manage in the tropics than in cold water regions.

Requirements and Activities

After identifying the planktonic organisms, it is obviously desirable to have information on their requirements and activities so that the contribution of the various plankters to the economy of the sea can be determined. Some information of this type has been gained by correlating plankton observations with hydrographic data (Sverdrup and Allen, 1939; Graham, 1941; Wood, 1954; Cassie, R. M., 1960; Cassie, V., 1960). Extensive sets of data, such as those collected by the Vityaz, should yield valuable results if analyzed in this way, especially now that computers are available to make the labor involved feasible.

The second approach to the study of the activities of phytoplankton is through laboratory study of cultures. Nutritional studies on a number of coastal and estuarine forms have been made (cf. Provasoli et al., 1957, of these studies for a review of the literature), and their extension to oceanic forms, as cultures of these become available, may be anticipated. Investigation of the pigmentation and photosynthesis of phytoplankters is an area that definitely requires more attention. Many measurements of the chlorophylls of plankton catches do not agree with the chlorophyll distribution in any organism so far studied. While some of this disagreement may be due to methodological difficulties, it appears at times to be outside the range of any probable experimental error. Studies of the photosynthesis of the organisms are woefully lacking, but this does not prevent generalizations about rates per unit of chlorophyll, etc., being common in the literature. Most of these generalizations are based on studies with Chlorophyta. However, the dominant organisms in most phytoplankton are members of the Chrysophyta, about which much less is known. The few studies that have been carried out with chrysophytes, e.g., those with the chrysomonads, Ochromonas malhamensis (Myers and Graham, 1956; Weis and Brown, 1959) and Ochromonas danica (Allen et al., 1960a), indicate differences from the well-known green plant pattern of characteristics. The chrysomonads appear more sensitive to unfavorable environmental conditions than the chlorophytes which have been used in photosynthetic studies.

HYDROGRAPHY AND PHYTOPLANKTON PRODUCTION*

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I. INTRODUCTION

In the greater part of the oceans, the supply of nutrients and the availability of light are the major abiotic environmental factors of significance in the production of organic matter. These factors are, in part, functions of the hydrographic conditions, in part of biological activity. Mathematical models have made it possible to understand the trend of production of organic matter by phytoplankton from a small number of environmental factors. Therefore, in this review, little will be said about the quality of the producers. The present knowledge of autecology of phytoplankton species rarely permits conclusions to be drawn from the specific composition of the community.

It is not possible to discuss adequately the knowledge concerning the dependence of phytoplankton production on hydrography by using productivity data alone. It is often necessary to consider indices of standing stock in areas where productivity data are lacking. Even observations on standing stock are scarce in tropical oceans, which make up slightly more than $\frac{2}{5}$ of the world ocean. Thus, this review will not exhaust the problems indicated by its title, but will contain examples of certain areas of investigation. Discussion of other aspects of this field of study can be found in Steele (1959), Steemann-Nielsen (1960b), and Strickland (1960).

The discussion will begin with a description of conditions in unstratified water during the initiation of the spring bloom, and the concepts for prediction of the timing of the bloom will be reviewed and applied to special cases. Conditions in deep waters of the temperate zone during summer stratification will be treated together with conditions in the tropical seas. In deep water, the importance of vertical mixing for nutrient supply will be stressed rather than recycling of nutrients in the mixed layer. This is in contrast to shallow waters where nutrients liberated on the sea-bed are readily available to the euphotic layer. The subsequent discussion is devoted to special topics which are treated individually. These are the problems of the occurrence of nutrient deficient plankton in old surface water of stratified seas, the retention of plankton in discontinuity layers, upwelling along the coasts of continents and in oceanic divergences, the effect of oceanic islands on productivity, the conditions in polar seas, and the influence of currents on plant populations. Estuaries and red tides will not be treated.

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II. SPRING BLOOMS IN DEEP WATER

Most of our knowledge of productivity has been gathered in the temperate and subarctic regions where the main event in the annual cycle of phytoplankton is the spring diatom bloom. It is now recognized that the increase of light available to the initial population determines the beginning of the bloom, not the nutrient enrichment of surface layers. During winter circulation, the mixed layer is deep and phytoplankton organisms are kept below the compensation depth for a large part of the time. The population, as a whole, is light deficient. A net daily increase in standing stock beneath a unit of surface area is not possible as respiration is greater than assimilation. The thickness of the mixed layer in which gain and loss of organic matter are equal is the "critical depth" (Sverdrup, 1953). If the mixed layer becomes shallower than the critical depth, sufficient light is made available to the plant population to allow an increase in standing stock. The critical depth has been shown to be five to ten times the compensation depth in Arctic and Subarctic water (Gran and Braarud, 1935; Sverdrup, 1953; Marshall, 1958); this value needs confirmation from other environments. The critical depth can be calculated from incident radiation, transparency, and the average compensation light intensity, determined experimentally. The value of the compensation light intensity (2.1×10^{-3} ly/min, 24-hour mean) used by Sverdrup (1953) and Marshall (1958) was taken from Jenkin's (1937) work with a Coscinodiscus culture. More recent data (Strickland, 1958b) compare rather favorably with this value. Nevertheless, more data on cultures as well as on mixed natural populations are urgently needed. The loss of organic matter by the phytoplankton is due not only to respiration of the algae, but to grazing and sinking as well. The loss by grazing can be determined experimentally and entered in the prediction of plant population increase as an increased "respiration rate" of the phytoplankton, if it can be assumed that the zooplankton population is distributed evenly within the mixed layer. Measurements on natural mixed populations might give, therefore, more useful estimates of the compensation light intensity than experiments on algal cultures, even though the conditions in the cultures can be defined more precisely. The loss due to sinking must be estimated.

Another approach to a prediction of the spring bloom has been offered by Riley (1957). He estimated from field observations in temperate waters that a mean radiation in the mixed layer of about 0.03 ly/min might be critical for the initiation of the increase of phytoplankton in spring. During autumn, nearly five times the mean radiation is needed to overcome the losses by higher respiration of phytoplankton and grazing (Riley, 1959a). Riley (1941b) had previously shown that, over Georges Bank, the rate of plant pigment increase was related to the quotient of depth of euphotic zone over depth of mixed layer.

It appears that light limits phytoplankton growth under oceanic conditions during winter from the polar through the temperate regions. This is also true for the poleward limits of the subtropics as shown by Riley (1957) for the North Central Sargasso Sea (35°N). The phytoplankton density may increase even during winter conditions in the temperate zone if the mixed layer has a neutral density gradient but is not turbulent. An example of a resulting uneven vertical distribution of phytoplankton in an apparently well mixed surface layer of the open Atlantic, has been given by Ryther and Hulbert (1960). It might be added that the general occurrence of intermediate O_2 maxima in the "wind stirred layer" of the ocean shows that very often physical forces do not act rapidly enough to overcome the effect of the small scale activity of plants and animals. The patchiness of plankton distribution is another illustration of this point.

A deep mixed layer also occurs in the subtropics during winter. However, there is usually sufficient incident light available for the critical depth to be greater than the depth of the mixed layer. Consequently near Bermuda (32°N), the main production is observed during and towards the end of the winter, a time when surface temperatures are low, vertical convection is deep, and fertilization of the euphotic zone occurs (Menzel and Ryther 1961b). However, the highest rate of production is observed when a slight stabilization has been established, according to original data kindly supplied by Dr. J. H. Ryther. Light still seems to control the rate of increase of the population.

The seasonal breakdown of stratification does not occur in the greater part of the tropical seas. The permanent discontinuity layer prevents fertilization of the surface water and pro-

duction stays at a low level throughout the year. Near Bermuda, the northern limit of this area is situated about 2 degrees south of the island (Ryther and Menzel, MS). Because light limits production during winter at 35°N (Riley, 1957), the region with winter flowering at this longitude is a belt not broader than about 300 miles.

Before turning to conditions in stratified waters after the spring bloom, it may be pointed out that the "spring" bloom is the only time of marked phytoplankton development in polar seas. For convenience, conditions in high latitudes are treated in a later chapter.

III. STRATIFIED SEAS

1. Conditions Over Deep Water

During summer stratification, the open seas of temperate regions are comparable to those tropical seas which are not influenced by monsoon winds and where radical seasonal changes are lacking. In both regions, a discontinuity layer is present, above which the nutrient content is low. In these seas, the role of vertical turbulence is a major factor in nutrient supply.

The dissipation of the spring bloom is due to nutrient depletion in the stabilized surface layers and loss of cells by sinking, and also to grazing by the herbivorous zooplankton. Cushing (1959) has suggested that, in higher latitudes, nutrient exhaustion is more likely to limit the bloom than grazing, owing to the considerable lag time for zooplankton development after the start of the phytoplankton bloom. At any rate, nutrient salts are subsequently lost from the euphotic zone by the buildup of organic matter, by its subsequent sinking, and by active downward transport by migrating zooplankton.

After the nutrient concentration is lowered, the rate of production will depend primarily on the rate of replenishment of nutrients but not necessarily on the amount found by direct analysis. An early attempt to formulate a nutrient budget for phosphorus was made by Ketchum (1947) for the Gulf of Maine. It was estimated that 73 percent of the phosphorus used annually was supplied by vertical transport, and 25 percent by regeneration in the surface layers. These figures are supported by the fact that Steele (1956) could predict plant production in a part of the northern North Sea reasonably well, assuming that all phosphate regeneration took place below the euphotic zone. The validity of this assumption was later confirmed by direct measurements with the C-14 method (Steele, 1957). It was estimated that 82 percent of the phosphorus used was supplied by vertical mixing, and 18 percent by regeneration in situ. High mixing rates during summer yielded high productivity due to the repeated fertilization of the stratified environment, thereby increasing markedly the value for the total annual production (Steele, 1958). Major variations in annual production were observed and related to variations in annual climatic conditions. It may be noted that Cushing (1949) and Harris (1959) have stressed the importance of recycling of nutrients in the euphotic zone by grazing.

Towards fall, stability is reduced by surface cooling and an increase in the supply of nutrients to the euphotic zone occurs. A fall bloom is promoted by a period of high mixing followed by a calm period, whereas gales, which break down stratification entirely, inhibit production due to the increased depth of the mixed layer. For this reason, the occurrence and magnitude of fall blooms will vary from year to year (Steele, 1958).

The effect of climatic conditions on annual production has been shown for the northern Sargasso Sea as well (Menzel and Ryther, 1961b). The amount of organic matter produced depends on the severity of the winter. In a cold winter, mixing reached greater depths and more nutrients were brought into the euphotic layer resulting in a higher productivity. Again, the recycling of nutrients above the summer thermocline is not as important as the effect of vertical transport.

Thus, in deep water, the distribution of productivity throughout the year is determined to a large extent by the rates of vertical mixing. As discussed previously, the mixing influences the availability of light to the population during spring, and also the supply of nutrients during summer. Because the level of production during the spring bloom depends on the mixing rates, higher rates removing more algae from the euphotic zone, it is to be expected that the ratio between spring and summer productivity, and the shape of the curve of annual production will vary both regionally and annually (Riley, 1941b; Steele, 1958). Most of the productivity meas-

urements available from offshore waters indicate that daily production during spring is two to three times that in later summer (Riley, 1941b; Ryther and Yentsch, 1958; Steele and Baird, 1961). However, Semina (1960) has reported that the maximum standing stock and production of phytoplankton occurs during fall in the subarctic North Pacific. It will be shown later that, in shallow waters, production in summer is usually greater than in the spring bloom.

It has been mentioned that permanent stratification is a characteristic feature of most of the tropical oceans, and fertilization of the surface layers by seasonal vertical mixing is not found. The resulting low production even during the "winter" was demonstrated by Ryther and Menzel (MS). Productivity figures of 0.05 – 0.10 (maximal 0.20) g C/m^2 day can be expected where the thin intermediate salinity maximum, in the upper part of the permanent discontinuity layer, indicates very weak vertical motions. The recycling of nutrients in these "old surface waters" may be of relatively greater importance than in temperate waters. Nutrient budgets have not been determined because of the difficulties in estimating eddy viscosity coefficients. However, if vertical mixing occurs, it can be expected to be more effective than recycling. In fact, the backbone of the distribution of productivity in tropical oceans is the oceanic circulation which will be discussed in the chapter on upwelling.

2. Conditions in Shallow Water

In this context, an area is regarded as shallow when the depth is smaller than the depth of the summer thermocline of the open sea. Important hydrographic features of shallow areas are the shallow depth of the mixed layer during winter and the small scale vertical turbulences throughout the year which add bottom water to surface layers. In the temperate zone, the critical depth is greater than the depth of the water even during winter if the water is moderately clear, and mid-winter blooms of plankton are possible. Several sets of observations have been mentioned by Riley (1957) in which winter blooms were observed in Cape Cod Bay, Long Island Sound, coastal waters south of Woods Hole and Block Island Sound. In each case, a radiation of 0.03 ly/min (24 hour mean) appeared to be critical.

As pointed out in the introduction, this review seldom considers the specific composition of the phytoplankton. The usefulness of knowledge about species composition for application of the critical depth concept is indicated by the observations of Conover (1956) on winter blooms in Long Island Sound. The usual winter flowering occurred three weeks earlier in 1954 than in 1953. The differences were apparently not related to conditions of light or stability. Conover suggested that the observed difference in water temperatures favored different diatom species. The dominant species in early 1954, Thalassiosira nordenskiöldii, was shown to have low light requirements, which presumably made an early flowering possible.

The organic matter synthesized during a bloom is either utilized by pelagic animals, or sinks to the sea-bed where consumption by bottom animals and mineralization by bacteria occur. In contrast to the open ocean, the inorganic nutrients set free at the bottom in shallow water are readily available to the algae. The rate of nutrient regeneration increases with rising temperature and is therefore higher during fall than in spring. Steemann-Nielsen and Hansen (1959b) have suggested that the bacteria cannot adapt to changing temperature as do phytoplankton and bottom invertebrates (see however Christopherson, 1955).

The annual distribution of production characteristic of shallow water of the temperate region can be seen from the results of four years of measurements of productivity in the Great Belt (Steemann-Nielsen, 1958b). The outstanding feature was that the average monthly production during the spring bloom was lower than during summer. The total summer production, which largely determined the total annual production, was linearly related to the average temperature from June to September. In long Island Sound, high daily production rates were measured in the summers of 1938 and 1939 (Riley, 1941a), whereas it can be deduced from a smaller number of experiments that, in 1953 and 1954, daily productivity was the same in spring as in summer (Conover, 1956). Of course, the consumption of organic matter is much higher during summer than during spring due to increased bacterial activity and a greater amount of zooplankton.

If a winter bloom depletes the nutrients before temperatures are high enough to permit a rapid regeneration of nutrients, production will decline. In Narragansett Sound, production decreased after the establishment of a shallow thermocline during spring (Pratt, 1959). Probably, the supply of nutrients from lower levels was considerably reduced. Later, the temperature of the surface layer increased and the increased rate of mineralization on the sea-bed above the depth of the thermocline became effective in stimulating production. Strong winds, weakening stratification, increased the mixing rate and led to a summer outburst of plankton (Smavda, 1957).

High productivity throughout the year is observed in all tropical near-shore waters because of the high bacterial activity in warm water (Steemann-Nielsen and Aabye-Jensen, 1957; see also Ichimura and Saijo, 1959, for the Kuroshio current). Productivity figures are not given because local conditions vary greatly, and the available data are too few to elucidate eventual trends.

Areas with a salinity stratification tend to be stratified throughout the year, and the transport of nutrients into the surface layer is reduced. Although these conditions are not confined to regions of shallow water, they are included in this section because of the shallow depth of the mixed layer. Production can proceed during winter because the mixed layer is shallow, but total annual production is low because the effect of recycling of nutrients in the mixed layer would be relatively unimportant. The conditions prevailing between the Baltic and the North Sea, as well as the Baltic itself, are an example from temperate zones (Steemann-Nielsen, 1940). Another example of low productivity associated with salinity stratification is found at Narsak in southern West Greenland, in the realm of the East Greenland current (Steemann-Nielsen, 1958b). Salinity stratification can be important in the tropics as well. In the equatorial rain belt, and in the areas influenced by it, the isothermal surface layer is often stabilized by salinity gradients. Accordingly, off Southwest India, productivity on the middle of the shelf during long times of the year is not markedly higher than reported from offshore areas. The highest productivity is observed in connection with large scale upwelling (unpubl. observations of Banse).

The discussion of conditions in shallow water can be concluded with some remarks on the seasonal distribution of phytoplankton standing stock in temperate latitudes. Cell counts and chlorophyll data usually show a peak during spring, and it is the common notion that the main event of the seasonal phytoplankton distribution is the diatom bloom in spring. However, if the cell size and the smaller amount of plasma in diatoms, as compared with dinoflagellates of the same dimensions, are taken into account, the spring bloom may lose its dominance, as shown by Lohmann (1908). His data for plasma volume, and hence for organic matter in phytoplankton for one year, show a trend similar to the four-year average of production observed by Steemann-Nielsen (1958b) at a locality with similar hydrographic conditions. In both cases, the spring bloom, which depends on the nutrients accumulated during winter, is not as prominent as previously thought; the summer production resulting from a high rate of nutrient regeneration is more effective. The estimates of standing stock from chlorophyll may be misleading (apart from the inclusion of dead chlorophyll) because dinoflagellate populations which prevail during summer have been shown by Gillbricht (1952) to have only half the ratio of chlorophyll/plasma volume as the diatoms.

The annual distribution of zooplankton biomass at the locality studied by Lohmann (1908) showed roughly the same trend as that of the phytoplankton. Although standing stock of the phytoplankton reflects the balance between production and loss due to sinking and grazing, it appears that a high rate of nutrient supply is sufficient to maintain a large phytoplankton population in the presence of high zooplankton standing stock, regardless of the nutrient concentration. Wattenberg and Meyer (1936), working at about the same locality as Lohmann (1908), reported zero phosphate at the surface from June onwards. The nutrient level is low also in highly eutrophic inshore areas, corresponding to about $^1/_5$ of the daily needs of the algal population (Steemann-Nielsen, 1958a). A similar situation was investigated by Ryther et al. (1958). On the other hand, in the regions of equatorial divergences, high productivity, high phytoplankton and zooplankton standing stock occur together, along with abundant nutrient concentrations and a presumably high rate of nutrient supply. A positive relation between plant pigment and nutrient content was also observed on Georges Bank during summer and in

January (Riley, 1941b); the usual inverse relationship occurred during spring. All the situations mentioned are believed to be stable but it is not yet clearly understood how these equilibria are maintained.

3. Phytoplankton-nutrient Concentration Relationships

Large areas of the warm seas, apart from upwelling areas and regions of divergences, are covered by old surface water which supports a low, fairly even production. The best known region of this kind is the Sargasso Sea. Riley (1957) believes that only a small fraction of the annual nutrient supply is derived from mixing across the deep permanent discontinuity layer. In consequence, regeneration of most of the nutrients must occur above this level. The inevitable loss of organic matter on which the deep-sea fauna depends, must be made good by advection. However, there may be a measurable gain of nitrogen from the atmosphere in certain cases (see below).

It has been suggested that there might occur in old surface water nutrient deficient plankton, with a ratio between nitrogen and phosphorus deviating from the normal one of 16:1 by atoms, and having very low turnover rates.* Before discussing the plankton itself, data on the N/P ratio in the sea may be mentioned. An increasing body of data indicates that the ratio in surface water is lower than 15:1 by atoms, the average ratio for the entire ocean (Steemann-Nielsen and Aabye-Jensen, 1957, Pacific; Ketchum et al., 1958b, Atlantic; Banse, unpublished, Laccadive Sea). As the average ratio in plankton is 16:1, the N in the water must reach zero before P does. However, after nitrate has been exhausted, phosphate values continue to decrease, as shown for the tropical Pacific (Steemann-Nielsen and Aabye-Jensen, 1957). This was explained as being due to a continuing supply of N which is used immediately. One source for N is a recycling rate higher than that of P, which is indicated by anomalously high N/P ratios usually found below the euphotic layer (Steemann-Nielsen and Aabye-Jensen, 1957) though it might not always hold true. Other sources are N_2 fixation by blue-green algae (Dugdale, et al. 1961) and, at the surface, the nitrate content of rain.

Only a few field observations on nutrient deficient plankton are available. Analysis of the N/P ratio in net plankton from Long Island Sound did not indicate a seasonal change (Harris and Riley, 1956). The ratio in the plankton was the normal one except in August, although the N/P ratio in the water during winter was much lower than 15:1, and was near zero during the summer months. In New England coastal waters, N and P were removed from the water in a ratio lower than 16:1 only during the summer when the N/P ratio in the water was very low (Ketchum et al., 1958b). During the other seasons, the elements were removed by the plankton in a ratio of 16:1 even though the ratio in the water was always below the normal one of 15:1. Unfortunately, the ratio of removal of N and P and the composition of phytoplankton could not be evaluated for the Sargasso Sea (Menzel and Ryther, 1960). The authors (1961a) showed that the algae were not able to remove all of the N and P present because Fe was limiting phytoplankton growth.

Nothing definite is known concerning the turnover rate in oligotrophic waters such as the Sargasso Sea. Steemann-Nielsen and Aabye-Jensen (1957) indicated that the rates may be half of eutrophic waters. In inshore and offshore waters of the northeast Atlantic, Currie (1958) compared C-14 assimilation with standing stock as measured by the total photosynthetic pigment content of the euphotic zone. The turnover rates differed by a factor of 2.5 without being dependent on the level of daily production. In a study using an incubator with high light intensity, Steele and Baird (1961) reported a twofold change in turnover rates during the year, the higher rates occurring at low nutrient concentrations. Similarly, McAllister et al. (1961) did not find a marked decrease in turnover rate after exhaustion of nutrients in their experimental study of a phytoplankton bloom run under near-natural conditions. Margalef (1958) has indicated that nutrient deficiency as known from monospecific cultures is apparently avoided in Mediterranean waters by successions of species adapted to the changing environment. This concept was previously suggested by Steemann-Nielsen and Hansen (1959a).

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*In the present paper the term "turnover rate" refers to the quotient net production over standing stock.

At present, it is not clear why the standing stock of phytoplankton in oligotrophic waters is always small as compared with the concentration of N and P in the water when the turnover rate at low nutrient levels is not greatly reduced. The standing stock might be controlled by grazing (Steemann-Nielsen, 1958a; Cushing, 1959), or phytoplankton production could be limited by elements other than nitrogen and phosphorous. Menzel and Ryther (1961a) have indicated that the algal production in the Sargasso Sea is limited by lack of Fe although the observed level of P and N is sufficient for about ten days of growth (also Ryther and Guillard, 1959). Si has been reported to be undetectable ($\leqq 0.5$ µg at/L Si) at the surface in most of the eastern tropical Pacific (Wooster and Cromwell, 1958).

Finally, it may be pointed out that even though the production per unit volume in oligotrophic water is low, the production per unit of surface is of the same order of magnitude as that of an eutrophic area. This is due to a reduction in the transparency and depth of the euphotic layer brought about by a high phytoplankton concentration in eutrophic waters (Steemann-Nielsen and Aabye-Jensen, 1957). It is likely that the eutrophic environment is more favorable for herbivorous zooplankton because of the higher concentration of food per unit volume.

4. Phytoplankton in Discontinuity Layers

Early observations on the accumulation of plankton in discontinuity layers were listed by Braarud and Klem (1931). More marine examples have become known since the introduction of transparency and scattering meters. From the Gullmarfjord, Pettersson (1934) reported a maximum of phytoplankton cells associated with a layer of high scattering in a halicline. The accumulation of plankton was said to correspond to the usual distribution of particles in a stratified medium. Krey (1954) studied the turbidity screen from the summer thermocline of the central and northern North Sea. Water samples were taken from the intermediate turbidity maximum, located by a transparency meter. Determinations were made of the weight of suspended matter and number of cells, and phytoplankton dry weight was calculated. Most phytoplankton was found in the layer of highest content of suspended matter which coincided with the layer of greatest light extinction. The phytoplankton often contributed more than 10 percent, in one case 50 percent of the weight of suspended matter, whereas in the clear water above and below the discontinuity layer, values less than 2 percent were usual.

The relatively greater retention of phytoplankton in the thermocline, as compared with detritus, was explained by Steele and Yentsch (1960) with two experiments in which a decrease of sinking rates occurred when slowly dividing cells of an old culture were placed in a nutrient enriched milieu. Usually, the water in and below a discontinuity layer is richer in nutrients than that of the surface layer. It is probable that physical factors, such as size and weight, are also involved in the retention of phytoplankton in discontinuity layers.

If the phytoplankton is retained in a discontinuity layer above compensation depth, it can reproduce under favorable conditions of nutrients and light. In this case, the distribution of assimilation with depth does not reflect the distribution of submarine light (Koblentz-Mishke, 1960).

The role of turbulence in settling rates has been discussed by Stommel (1949). Convection cells may retain particles, thus allowing the algae to remain longer in well illuminated layers. With non-motile plants, the absorption of nutrients is aided by a rapid sinking rate (Munk and Riley, 1952).

IV. UPWELLING

For convenience, this section will be divided into a discussion of the rising of deep water along oceanic divergences and of upwelling along the coasts of continents. The island mass effect will be included at the end of the present section as this phenomenon may be due to increased vertical mixing as islands are approached as well as to the effect of mineralization on the sea-bed in relatively shallow waters.

It was stated earlier that the backbone of the distribution of oceanic productivity in lower latitudes is the oceanic circulation and that the effect of recycling of nutrients in surface layers

is relatively unimportant. This is also true when upwelling is considered. Because few productivity measurements are available, the following discussion will depend to a large extent upon standing stock studies.

A direct relation between phosphate and nannoplankton distribution (Hentschel and Wattenberg, 1930) and metazoa (Hentschel, 1933) occurs in the tropical Atlantic. The phosphate distribution in turn is related to the depth of the permanent discontinuity layer (Defant, see Dietrich and Kalle, 1957, Fig. 130), shallow depths corresponding to high phosphate values in the surface layer. Wattenberg (1957) pointed out that the area of high phosphate content extending downstream from the upwelling region off Southwest Africa is caused by local divergences, not by advection.

From the eastern Pacific, further examples of the dependence of production on hydrography are available. There is a close relationship between the topography of the sea surface (Jerlov, 1953b), or depth of the thermocline (Brandhorst, 1958), to the particle content (Jerlov) and to the zooplankton volume (net plankton, Brandhorst). The particle content in offshore waters may serve as a very rough approximation of the phytoplankton content (Gillbricht, 1959). Apart from the upwelling areas near the coast, high particle contents are found below the equator at the equatorial divergence and at the divergence between counter current and north equatorial current. The longitudinal sections of the "Albatross" on which the publication of Jerlov is based (see also Sverdrup et al., 1942, Fig. 198) show that the plankton distribution is not caused by transport of nutrients from the upwelling area off Central America, but is due to local divergence. In the equatorial Pacific, between 155° and 175°W, the inverse relation between depth of the thermocline, phosphate content of the surface layer, and net zooplankton abundance has been observed by King and Demond (1953). The same was emphasized by Holmes (1958a) who published average productivity measurements for the eastern Pacific. The available data indicate that the equatorial divergence causes a higher productivity than the divergence between the counter current and the north equatorial current (Austin, 1960). In the Indian Ocean, Jerlov (1953a) has reported a high particle content in the divergence between the south equatorial current and the counter-current, and in the region of the equatorial divergence.

The daily primary production near the equatorial divergences ranges from 0.2 – 0.5 g C/m^2 (Steemann-Nielsen and Aabye-Jensen, 1957), but little is known of seasonal variations. The material of King and Demond (1953) from the central Pacific has been collected during several months, but does not elucidate the effect of seasonal variations in the extent and strength of the trade winds, or the counter currents on primary productivity in the tropics. Hasle (1959) has pointed out that the Secchi-disc readings change during parts of the year in the equatorial Pacific. Other data from the eastern tropical Pacific have been discussed by Wooster and Cromwell (1958). It is believed that the reversal of currents in the open Indian Ocean caused by the changing monsoons has a profound effect on the productivity.

The most intensive upwelling is found near-shore at the eastern side of the trade wind belts. In these regions, very high daily rates of oceanic productivity have been observed (3.8 g C/m^2 in Walvis Bay, Steemann-Nielsen and Aabye-Jensen, 1957). Otherwise, little is known of the biological aspects of production in coastal upwelling areas.

A detailed account of net plankton distribution off California offers further confirmation for the inverse relation between thermocline depth and plankton content (Sverdrup and Allen, 1939). The new surface water found over areas of ascending motion with shallow thermoclines usually contained more cells than nearby regions with old surface water. However, some areas with supposedly recent upwelled water contained little phytoplankton, a situation similar to the low productivity measurements found by Steemann-Nielsen and Aabye-Jensen (1957) off Southwest Africa. A possible explanation for this is the assumption of a lag phase for phytoplankton development due to the absence of some growth promoter substance in the upwelled water (discussion in Strickland, 1960). Certainly, the problem of seeding the cool water, and the physical effects of dilution of the initial population by newly upwelled water, along with vertical instability, are significant components of the problem.

All large upwelling areas appear to have a complex hydrography which makes the interpretation of biological observations difficult. This can be seen from the recent account of the Benguela Current (Hart and Currie, 1960). Owing to recent stratification after a period of active upwelling, very high surface nutrient concentrations may be found in strongly stratified

water. Unbalanced situations of this kind must be elucidated by time series observations with frequent sampling, supported by sections through the area.

A remark will be made about the island mass effect. Recently, new attention has been drawn to the fact that the increase of phytoplankton standing stock near the shores of the ocean can be observed near oceanic islands as well. In an early study, Hentschel (1933) showed that not only downstream from small islands, but also windward, an increase of phytoplankton is noticeable although no neritic species appear. Even in the Bay of St. Helena, the species composition of the phytoplankton was similar to that of the open ocean but the cell counts were doubled. The reason for the increased plankton content may be the increased vertical turbulence, and the effect of benthic biological activity as discussed earlier.

Doty and Oguri (1956) have observed windward of the Hawaiian island of Oahu, an increase of carbon fixation of two orders of magnitude from 15 miles out in the open sea into a bay. Menzel (MS) has shown that carbon fixation increased by a factor of 2-6 as shore was approached in three sections to Castle Harbor, Bermuda from a point 23 miles offshore. However, the increase in standing crop of phytoplankton was not as great and the nutrient concentration did not show an increase except within Castle Harbor. The rate of carbon fixation per unit of chlorophyll was significantly higher inshore. This may indicate physiological differences between inshore and offshore populations if the assumption is correct that nitrogen and phosphorous are not limiting in these waters (Ryther and Guillard, 1959). As mentioned earlier, Currie (1958) did not find a definite increase in the rate of carbon fixation per unit of photosynthetic pigment when approaching the Iberian and North African coasts from fairly oligotrophic waters.

V. POLAR SEAS

Usually, in polar seas, a single phytoplankton bloom is observed each year. The peak of production in the Arctic, under the permanent ice-pack, occurs in July or August. The disappearance of the snow cover and the appearance of numerous meltwater ponds allow sufficient light for phytoplankton growth to pass through the ice (cf. the net plankton data of Shirshov 1938 and the chlorophyll and C-14 data of English MS). Braarud (1935) has suggested that regional summer variations of the average cloud cover may be a cause for considerable regional differences in annual production. In any case, the few measurements of productivity available show that annual production is very low. This is to be expected due to the unfavorable environmental conditions.

Outside the permanent ice-pack, the opening of the ice itself in late spring or early summer makes available sufficient light for plant growth and initiates the phytoplankton bloom. Nutrients are quickly exhausted because the surface layer is stratified and consequently, the bloom is of short duration. In temperate latitudes, sufficient incident light may be available before the ice breaks up, in which case, a phytoplankton bloom will develop if the mixed layer is thin (Steemann-Nielsen, 1951b).

Eight and one-half percent of the world oceans are situated within the Antarctic convergence, i.e. in the Antarctic region proper as pointed out by Hart (1942). The Antarctic convergence is located at about 50°S in the Atlantic and Indian sectors but is found farther south in the Pacific. As the summers are much cooler than in the northern hemisphere at corresponding latitudes, polar conditions with pack and drift-ice prevail in lower latitudes, than in the Arctic.

Little is known concerning the productivity of the Antarctic region. The dependence of the phytoplankton bloom on stratification has been shown for the Weddell Sea by Gran (1932). In the Bellingshausen Sea, Hart (1934) has reported greatest phytoplankton catches from areas with melting pack-ice. Because stratification sets in later than in the northern hemisphere at similar latitudes, the spring increase of phytoplankton is accordingly later. In South Georgia, the great increase is observed in November whereas at 54° latitude in the boreal region, the increase occurs from March to May depending upon hydrographic conditions (net plankton data from Colebrook and Robinson, 1961).

Apparently, the euphotic layer is shallow. Gran (1932) observed the main concentration of diatoms in the upper 25 m but a slight decrease of phosphate was noted at 40 m. Hart (1942),

in an investigation of centrifuged samples from more than 100 stations throughout the Antarctic found the maximum cell numbers at the surface on 25 percent of the stations, at 5 m on 44 percent, and at 10 m on 11 percent. These data indicate that the euphotic layer seldom exceeds 50 m. Further evidence was produced by a longitudinal section in the Pacific sector (Hasle, 1956), although the maximum cell numbers often occurred at 25 m. It is improbable that the depth of the euphotic zone is limited by the concentration of phytoplankton, but is more likely due to the low intensity of incident light. The greater part of the ice-free area has a heavy cloud cover. It is also doubtful that nutrients limit production on a large scale because of insufficient light (Gran, 1931). Although the surface water is well stratified during summer (Deacon, 1937), phosphate and nitrate are abundant but silicate may drop to low values (Clowes, 1938). The influence of the divergences within the Antarctic region on production have not been studied in detail but might yield a better understanding of the conditions in the Antarctic water ring (Koopmann, 1953; Beklemishev, 1960).

Hentschel (1933) reported low concentrations of cells, in the order of 100,000 – 200,000 cells/L. However, it has been recommended that these values be multiplied by a factor of three (Steemann-Nielsen and Aabye-Jensen, 1957, on the basis of previous experiments). Only one set of productivity measurements is available (Klyashtorin, 1960). Assimilation values between 5 and 10 (maximal 20) mg C/m^3 day were found in 24 hour experiments with surface water. From these data, the writers of this paper have estimated a daily production, for a euphotic zone of 50 m depth, of 0.2 – 0.5 g C/m^2, a range similar to that known from the equatorial divergences. Because production is limited to about three months near the Antarctic, continent, and to seven to eight months in the northernmost parts of the Antarctic region, Hart (1942) has suggested that Antarctic waters might not be as productive as previously thought. The biomass of the bottom fauna of Antarctic waters is not exceedingly large either (Zenkevitch et al., 1960).

The large standing stocks of plankton found in the neritic realm of the Antarctic cannot be explained by hydrographic factors (Hart, 1942). In deep waters near South Georgia, the average plant pigment values of net plankton during the season of maximum growth were ten times higher than in the open ocean. 10 degrees to the south, in deep waters of the Gerlache and Bransfield Straits, chlorophyll-a values of 5-20 mg/cm^3 were reported late in the growing season (Burkholder and Sieburth, 1961). Because nutrients do not limit production in the Antarctic, the high standing stock near land cannot be caused by regeneration of phosphate and nitrate on the sea-bed. Also, the standing stock of phytoplankton is high far beyond the shelf (Hart, 1934). A neritic species composition prevails near the land and the ice-pack, in both the Antarctic and Arctic.

VI. HORIZONTAL WATER MOVEMENTS

The role of ocean currents in the distribution of phytoplankton has been discussed for many decades. Recent investigations from the North Sea (Braarud et al., 1953) and from the Norwegian Sea (Paasche, 1960a) may be mentioned. In both areas, hydrographically defined subregions are inhabited by different populations. This is due partly to difference in time of onset of the seasonal succession of populations in individual subregions. The other reason for population variation is the "seeding" effect brought about by advection. The distribution of *Coccolithus huxleyi* in the North Sea depends upon the variable spreading of an initial population by fresh influxes of Atlantic water (Braarud et al., 1953). Annual differences in composition of the populations in the Atlantic water of the Norwegian Sea have likewise been attributed to differences in the initial stock, dependent upon the biological state of the Atlantic water when entering the Norwegian Sea, and to its subsequent spreading (Paasche, 1960a). However, in both papers, it is emphasized that the timing of the spring bloom, and the amount of production, can be explained by environmental factors such as turbulence (see also Gran, 1902). At present, the variations in timing cannot be related to the presence of different species.

The study by Conover (1956) in Long Island Sound shows that, with experimental knowledge of the autecology of species, it is possible to be specific rather than to ascribe the dependence of productivity to hydrographic conditions alone. In addition to the Norwegian observations, the

annual surveys of net phytoplankton by Allen (1928, 1936) at La Jolla, Cupp (1937) in Alaskan waters, and Subrahmanyan (1959) off Calcutta show considerable annual variation in species dominance. Considerable experimental work is needed to elucidate the autecology of the important species before species counts can be applied to productivity studies. However, even with more biological information on the species level, the assimilation experiments and chlorophyll determinations along with chemical data will continue to be useful and attractive tools in the description of biological properties of sea water.

TABLE 1 — Phytoplankton off Southern California

I. DIATOMS

Actinoptychus splendens
Actinoptychus undulatus
Asterionella japonica*
Asteromphalus heptactis
Asteromphalus hookeri
Bacteriastrum elongatum
Biddulphia aurita
Biddulphia extensa
Biddulphia mobiliensis
Cerataulina bergonii
Chaetoceros criophilum
Chaetoceros debile*
Chaetoceros gracile
Chaetoceros neapolitanum
Chaetoceros pendulum
Chaetoceros tetrastichon
Chaetoceros simile
Coscinosira polychorda
Ditylum brightwellii
Eucampia zoodiacus*
Ethmodiscus rex
Lauderia borealis
Licmophora lyngbyei
Lithodesmium undulatum
Nitzschia seriata*
Planktoniella sol
Rhizosolenia alata
Rhizosolenia calcaravis
Rhizosolenia faeroensis
Rhizosolenia robusta
Rhizosolenia setigera
Skeletonema costatum*
Stephanopyxis tunis
Thalassiothrix frauenfeldii
Thalassiothrix longissima

II. DINOFLAGELLATES

Ceratium arietinum
Ceratium azoricum
Ceratium candelabrum
Ceratium contortum
Ceratium extensum
Ceratium furca*
Ceratium fusus
Ceratium kofoidii
Ceratium lineatum
Ceratium longipes
Ceratium longirostrum
Ceratium macroceros
Ceratium pentagonum
Ceratium pulchellum
Ceratium trichoceros
Ceratium tripos*
Ceratium spp.
Dinophysis acuminata
Dinophysis acuta
Dinophysis arctica
Dinophysis caudata
Dinophysis ellipsoidea
Dinophysis hastata
Dinophysis spp.
Goniaulax catenella
Goniaulax polyedra*
Goniaulax spp.
Gymnodium spp.
Noctiluca miliaris
Oxytoxum spp.
Peridinium crassipes
Peridinium depressum
Peridinium divergens
Peridinium globulus
Peridinium granii
Peridinium minitum
Peridinium oceanicum
Peridinium pentagonum
Peridinium pyriforme
Peridinium steinii
Peridinium spp.
Phalacroma rudgei
Podolampes bipes
Prorocentrum dentatum
Prorocentrum micans*
Pyrocystis lumula

* = dominant species

W. E. Allen, Amer. Midland Nat. 26, 603-635 (1941).
———, Bull. Scripps Inst. Oceanogr. 1, 357-401 (1928)

TABLE 2 — Phytoplankton of the Puget Sound Area

Part I. Diatoms

– OCEANIC –

Arctic

Chaetoceros convolutus
Chaetoceros decipiens
Lyalodiscus subtilis
Nitzschia seriata
Rhizosolenia semispina

Temperate

Asteromphalus heptactis
Bacteriastrum delicatulum
Corethron hystrix
Coscinodiscus centralis
Coscinodiscus concinus
Coscinodiscus excentricus
Coscinodiscus radiatus
Coscinodiscus stellaris
Rhizosolenia alata
Rhizosolenia styliformic

– NERITIC –

Arctic

Biddulphia aurita
Chaetoceros gracilis
Thalassiosira nordenskioeldii

North Temperate

Asterionella kariana
Biddulphia longicruris
Chaetoceros affinis
Chaetoceros compressus
Chaetoceros concavicornis
Chaetoceros danicus
Chaetoceros debilis
Chaetoceros diadema
Chaetoceros laciniosus
Chaetoceros pseudocrinitus
Chaetoceros radicans
Chaetoceros similis
Chaetoceros teres
Chaetoceros vanheurckii
Coscinosira podychorda
Leptocylindrus danicus
Leptocylindrus minimus
Nitzschia delicatissima
Rhizosolenia fragilissima
Rhizosolenia setigera
Rhizosolenia stolterfothii
Stephanopyxis nipponica
Skeletonema costatum
Thalassiosira condensata
Thalassiosira decipiens
Thalassiothrix nitzschioides

South Temperate

Asterionella japonica
Cerataulina bergonii
Chaetoceros crucifer
Chaetoceros didymus
Chaetoceros eibenii
Chaetoceros lorenzianus
Coscinodiscus granii
Ditylum brightwelli
Eucampia zoodiacus
Nitzschia paradoxa
Rhizosolenia delicatula
Stephanopyxis palmeriana
Thalassiosira rotula

Tychopelagic

Actinoptychus undulatus
Biddulphia laevis
Nitzschia closterium
Paralia sulcata
Pleurosigma fasciola

Distribution uncertain

Chaetoceros decipiens
Coscinodiscus wailesii
Dactyliosolen mediterraneus
Rhizosolenia hebetata
Rhizosolenia stolterfothii
Thalassiosira aestivalis
Thalassiosira nordenskioeldii
Tropidoneis antarctica

TABLE 2—Continued

Part II. Dinoflagellates

Ceratium fusus	Noctiluca scintillans
Ceratium tripos	Oxytoxum diploconus
Dinophysis acuminata	Peridinium conicum
Dinophysis acuta	Peridinium depressum
Dinophysis ellipsoides	Peridinium divergens
Dinophysis sphaerica	Peridinium micrapium
Exuviella perforata	Peridinium obtusum
Goniaulax spinifera	Phalacroma rotundatum
Gymnodiunium lunula	Protoceratium reticulatum

L. D. Phifer Univ. of Wash., Publ. in Oceanogr. 1, 39-81 (1933).
T. G. Thompson and L. D. Phifer, ibid. 1, 83-96 (1934).

TABLE 3—Nannoplankton of a British Columbia Fjord

CHRYSOPHYCEAE

Chromulina sp.
Ochromonas (?) vallesiaca
Chrysochromulina sp.
Chrysamoeba nana*
Microsportella fiordensis*

XANTHOPHYCEAE

Xanthomonas (nov. gen.) thalassoides*
Pseudomicrosportella (nov. gen.) ornata*

CHLOROPHYCEAE

Anisomonas astigmatica*
Thalassomonas exurgens

*New species.

Robert F. Scagel and Janet R. Stein. Can. Jour. Bot. in press.

TABLE 4 — Phytoplankton of the Northeast Pacific

In open Pacific

Nannoplankton	Net phytoplankton
Coccolithophores	Ceratium fusus
	Ceratium tripos
	Chaetoceros neapolitanus
	Chaetoceros peruvianus
	Coscinodiscus marginatus
	Pontosphaera huxleyi

Near Scotch Cap Light, Unimak Island

I. Diatoms

OCEANIC

Arctic

Chaetoceros convolutus
Chaetoceros decipiens
Corethron valdiviae
Nitzschia seriata
Rhizosolenia obtusa
Rhizosolenia semispina
Thalassiothrix longissima

Temperate

Asteromphalus heptactis
Bacteriastrum delicatulum
Chaetoceros peruvianus
Corethron hystrix
Coscinodiscus centralis
Coscinodiscus excentricus
Coscinodiscus radiatus
Rhizosolenia alata
Rhizosolenia styliformis
Thalassiosira subtilis
Thalassiothrix frauenfeldii

NERITIC

Arctic

Biddulphia aurita
Chaetoceros furcellatus
Chaetoceros mitra
Fragilaria islandica
Streptotheca thamesis
Thalassiosira gravida
Thalassiosira nordenskiöldii

Temperate – Northerly

Asterionella kariana
Aulacodiscus argus
Biddulphia longicruris
Chaetoceros compressus
Chaetoceros concavicornis
Chaetoceros constrictus
Chaetoceros danicus
Chaetoceros debilis
Chaetoceros pseudocrinitus
Chaetoceros radicans
Chaetoceros similis
Chaetoceros socialis
Chaetoceros subsecundus
Coscinodiscus nitidus
Coscinosira polychorda
Leptocylindrus danicus
Leptocylindrus minimus
Nitzschia delicatissima
Rhizosolenia setigera
Rhizosolenia stolterfothii
Skeletonema costatum
Stephanopyxis nipponica
Thalassionema nitzschioides
Thalassiosira condensata
Thalassiosira decipiens

Temperate – Southerly

Asterionella japonica
Biddulphia mobiliensis
Cerataulina bergonii
Chaetoceros affinis
Chaetoceros curvisetus
Coscinodiscus granii
Ditylum brightwellii
Eucampia zoodiacus
Grammatophora marina
Lauderia borealis

TABLE 4—Continued

Chaetoceros didymus	Nitzschia pungens
Chaetoceros laciniosus	Rhizosolenia delicatula
Chaetoceros lorenzianus	Stephanopyxis palmeriana
Chaetoceros simplex	Thalassiosira rotula

TYCHOPELAGIC

Achnanthes sp.	Licmophora lyngbyei
Actinoptychus undulatus	Licmophora sp.
Biddulphia pulchella	Melosira sp.
Cocconeis	Melosira sulcata
Fragilaria sp.	Nitzschia closterium
Fragilaria striatula	Pleurosigma sp.
Grammatophora	Rhabdonema arcuatum
Isthmia nervosa	Striatella unipunctata

II. Dinoflagellates

Ceratium furca	Dinophysis rotundata
Ceratium fusus	Dinophysis sp.
Ceratium longipes	Goniaulax sp.
Ceratium pentagonum	Peridinium crassipes
Ceratium sp.	Peridinium depressum
Ceratium tripos	Peridinium divergens
Dinophysis acuminata	Peridinium ovatum
Dinophysis acuta	Peridinium pentagonum
Dinophysis arctica	Peridinium sp.
Dinophysis caudata	Peridinium steinii
Dinophysis ellipsoides	Phalacroma rudgei
Dinophysis ovum	Prorocentrum micans

In the Bering Sea

Achnanthes longipes	Chaetoceros teres
Asteromphalus sp.	Hyalochaete spp.
Biddulphia aurita	Corethron hystrix
Chaetoceros atlanticus	Coscinodiscus spp.
Chaetoceros convolutus	Denticula sp.
Chaetoceros concavicornis	Fragilaria spp.
Chaetoceros decipiens	Melosira sulcata
Chaetoceros compressus	Nitzschia seriata
Chaetoceros didymus	Phaeoceros spp.
Chaetoceros constrictus	Rhizosolenia hebetata f. semispina
Chaetoceros subsecundus	Rhizosolenia heb. f. hiemalis
Chaetoceros seiracanthus	Strephanopyxis nipponica
Chaetoceros debilis	Thallassiosira nordenskioeldii
Chaetoceros radicans	Thallassiosira decipiens
Chaetoceros furcellatus	Thalassiothrix longissima

E. E. Cupp, Bull. Scripps Inst. Oceanogr. 4, 71-100 (1937).

C. D. McAllister, T. R. Parson and J. D. H. Strickland, J. du Conseil 25, 240-259 (1960).

K. Karohji, Bull. Fac. Fish. Hokkaido Univ. 8, 243-252 (1958).

TABLE 5 — PHYTOPLANKTON OF THE EASTERN PACIFIC

A. North of 40°N

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
	48°48'N 175°35'W	47°18.9'N 175°57'W	45°50.8'N 175°45.2'W	44°05.3'N 175°47.2'W	42°28.4'N 175°44'W	45°52.4'N 160°10'W	47°27.2'N 160°03.4'W	53°29.2'N 159°52.4'W	54°22.3'N 159°29.8'W	54°24.6'N 157°06'W	54°26.7'N 155°34.8'W	54°26.8'N 154°17'W	54°23.8'N 150°46.3'W	54°22.4'N 149°09'W	54°21.9'N 147°42.4'W	55°46.8'N 145°26.1'W	54°24'N 137°03.7'W	54°23.8'N 134°41.4'W	54°24'N 133°49.7'W	49°26.6'N 128°53.4'W	49°30.7'N 128°41.7'W	49°33'N 131°24.6'W	49°35.5'N 133°56.7'W	49°33.5'N 136°54.3'W	49°43.2'N 144°06'W	48°17.2'N 144°13.1'W	46°52.7'N 144°04'W	44°58.3'N 144°02'W	44°50.8'N 140°14.8'W	44°59.5'N 137°57.4'W	44°56.1'N 135°35.5'W	44°57.6'N 131°05'W	44°58'N 128°50.3'W	44°51.7'N 125°04'W
Actinoptychus undulatus																	+																	
Asteromphalus heptactis												+	+			+	+		+								+							
Bacteriastrum delicatulum																	+	+					+											
Biddulphia aurita						+																+												
Ceratium buceros																		+																
Ceratium carriense																																	+	
Ceratium declinatun																							+	+	+	+	+	+		+				
Ceratium extensum																								+									+	
Ceratium furca																								+										
Ceratium fusus	+			+			+									+								+	+	+					+	+		
Ceratium fusus var. seta		+	+			+	+				+	+										+												
Ceratium longipes			+		+				+	+		+	+			+																		
Ceratium lumula																							+											
Ceratium macroceros								+																					+		+		+	
Ceratium macroceros var. gallicum																																		
Ceratium massiliense																	+					+	+	+	+		+	+	+	+				
Ceratium pentagonum						+						+												+		+					+			
Ceratium pulchellum																		+																
Ceratium trichoceros																		+					+				+						+	
Ceratium tripos						+			+		+	+	+	+																				
Ceratium tripos f. molle										+																								
Chaetoceros affinis																					+		+											
Chaetoceros atlanticus	+	+	+			+	+		+	+	+	+	+	+	+	+	+	+					+		+	+	+	+	+	+				
Chaetoceros concavicornis		+		+				+		+				+						+	+					+	+					+		+
Chaetoceros concavicornis f. volans						+	+					+																						
Chaetoceros constrictus																																		
Chaetoceros costatus																																		
Chaetoceros convolutus			+			+			+		+							+											+	+				
Chaetoceros decipiens									+	+	+	+		+			+	+		+	+		+											
Chaetoceros peruvianus																								+										
Chaetoceros teres																					+		+											
Corethron hystrix			+	+		+								+																				
Coscinodiscus asteromphalus									+	+	+	+								+		+												+
Coscinodiscus centralis																							+				+							
Coscinodiscus concinnus																					+													
Coscinodiscus curvulatus						+											+																	
Coscinodiscus excentricus						+																												
Coscinodiscus granii									+																									
Coscinodiscus lineatis													+																					

TABLE 5 — PHYTOPLANKTON OF THE EASTERN PACIFIC

A. North of 40°N

	1 48°48'N 175°35'W	2 47°18.9'N 175°57'W	3 45°50.8'N 175°45.2'W	4 44°05.3'N 175°47.2'W	5 42°28.4'N 175°44'W	6 45°52.4'N 160°10'W	7 47°27.2'N 160°03.4'W	8 53°29.2'N 159°52.4'W	9 54°22.3'N 159°29.8'W	10 54°24.6'N 157°06'W	11 54°26.7'N 155°34.8'W	12 54°26.8'N 154°17'W	13 54°23.8'N 150°46.3'W	14 54°22.4'N 149°09'W	15 54°21.9'N 147°42.4'W	16 55°46.8'N 145°26.1'W	17 54°24'N 137°03.7'W	18 54°23.8'N 134°41.4'W	19 54°24'N 133°49.7'W	20 49°26.6'N 128°53.4'W	21 49°30.7'N 128°41.7'W	22 49°33'N 131°24.6'W	23 49°35.5'N 133°56.7'W	24 49°33.5'N 136°54.3'W	25 49°43.2'N 144°06'W	26 48°17.2'N 144°13.1'W	27 46°52.7'N 144°04'W	28 44°58.3'N 144°02'W	29 44°50.8'N 140°14.8'W	30 44°59.5'N 137°57.4'W	31 44°56.1'N 135°35.5'W	32 44°57.6'N 131°05'W	33 44°58'N 128°50.3'W	34 44°51.7'N 125°04'W
Coscinodiscus marginatus								+																									+	
Coscinodiscus oculus iridis										+		+		+							+	+	+		+									
Coscinodiscus perforatus												+					+																	
Coscinodiscus perforatus var. cellulosa									+			+																						
Coscinodiscus wailesii									+			+					+				+	+												
Denticula marina	+	+	+			+	+					+	+	+	+										+	+	+					+		
Dinophysis tripos																																+		
Dinophysis sp.																																+		
Distephanus sp.						+						+	+				+			+														
Ditylum brightwellii												+																						
Fragilaria sp.										+																	+							
Goniaulax polyedra																																+		
Goniaulax sp.																															+	+		
Guinardia flaccida																														+				
Hemidiscus cuneiformis																																	+	
Nitzschia seriata									+								+		+			+				+						+		
Oscillatoria thiebautii					+																						+							
Peridinium solidicorne																																		
Peridinium sp.																																+		
Phalacroma sp.																															+	+		
Pseudoeunotia doliolus											+	+	+			+										+	+	+	+	+				
Pyrocystis pseudonoctiluca					+		+																					+	+	+			+	+
Pyrocystis rhomboides																												+						
Rhizosolenia alata			+							+		+								+			+	+	+	+	+	+		+				+
Rhizosolenia alata f. curvirostris						+					+					+		+																
Rhizosolenia calcar-avis																				+														+
Rhizosolenia hebetata												+		+				+		+		+	+				+							+
Rhizosolenia hebetata f. hiemalis		+	+														+																	
Rhizosolenia robusta																				+	+		+											+
Rhizosolenia setigera												+																						
Rhizosolenia styliformis					+	+				+	+	+	+	+	+	+				+			+		+	+	+	+				+		+
Skeletonema costatum																																		
Stephanopyxis nipponica											+	+																						
Thalassionema nitzschoides									+		+	+					+						+											
Thalassiosira sp.																										+		+		+				
Thalassiothrix delicatula				+																											+			+
Thalassiothrix frauenfeldianum									+			+						+		+														
Thalassiothrix longissima	+		+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+				

TABLE 5 — PHYTOPLANKTON OF THE EASTERN PACIFIC

B. 19 to 40°N

Species	1 40°24.1'N 175°41.8'W	2 39°26.9'N 176°02.4'W	3 37°48.8'N 175°56.9'W	4 36°28.7'N 175°57.5'W	5 35°03.0'N 176°00.4'W	6 34°59.8'N 172°56.5'W	7 34°59.4'N 169°37.1'W	8 35°01.6'N 166°27.7'W	9 34°58.4'N 163°05.4'W	10 40°00.3'N 125°08.2'W	11 40°01.0'N 127°39.0'W	12 40°01.4'N 129°16.0'W	13 40°03.0'N 131°26.7'W	14 40°03.0'N 133°56.6'W	15 40°20.0'N 135°46.9'W	16 40°03.5'N 137°54.4'W	17 49°04.9'N 140°01.9'W	18 37°35.1'N 139°59.7'W	19 36°06.3'N 139°55.5'W	20 35°06.8'N 137°53.0'W	21 35°00.2'N 136°01.7'W	22 34°59.8'N 134°01.8'W	23 34°5.4'N 132°02.0'W	24 34°57.0'N 130°00.0'W	25 34°51.1'N 128°01.4'W	26 34°58.3'N	27 35°02.3'N 121°43.5'W	28 30°00.0'N 118°02.8'W	29 29°58.4'N 120°43.0'W	30 30°00.3'N 123°14.6'W	31 30°00.3'N 125°54.0'W
Amphisolenia bidentata																				+	+	+									+
Amphisolenia rectangulata																															
Amphisolenia spinulosa																															
Amphisolenia trinax																															
Amphisolenia zimmermanni																															
Amphisolenia sp.																															
Asterolampa marylandica																			+			+								+	+
Asteromphalus sp.																															
Bacteriastrum delicatulum								+											+												
Ceratium arietinum f. detortum						+																									
Ceratium belose																											+	+	+		
Ceratium buceros																															
Ceratium candelabrum																											+	+			+
Ceratium carriense									+													+						+	+		
Ceratium contortum																															
Ceratium declinatum													+						+	+				+				+			+
Ceratium deflexum																													+		+
Ceratium extensum			+		+	+	+	+	+	+	+	+	+					+	+		+	+		+		+	+	+	+	+	+
Ceratium euarcuatum																															
Ceratium falcatum									+																						
Ceratium fusus													+							+						+	+	+			+
Ceratium fusus var. seta				+	+	+	+																								
Ceratium gravidum																				+								+			+
Ceratium hexacantum f. contortum																												+		+	
Ceratium hexacantum f. spirale																															
Ceratium inflatum																															
Ceratium karstenii													+	+	+																
Ceratium longinum																															
Ceratium longirostrum						+	+		+									+		+								+			
Ceratium lumula																															
Ceratium macroceros						+	+			+									+						+	+	+	+	+		+
Ceratium macroceros var. gallicum									+					+					+												+
Ceratium massiliense				+	+			+	+	+	+	+		+	+	+		+	+		+	+		+	+	+	+	+		+	+
Ceratium pentagonum										+																+	+	+			
Ceratium pulchellum																															
Ceratium ranipes																															
Ceratium trichoceros						+	+	+	+		+	+	+	+				+	+	+	+			+	+		+	+	+		+
Ceratium vultus																				+					+			+		+	+
Ceratocorys horrida																			+									+		+	
Chaetoceros affinis																			+												
Chaetoceros coarctatus						+		+	+				+		+				+	+	+	+		+			+			+	+
Chaetoceros concaviformis										+									+												
Chaetoceros convolutus													+																		
Chaetoceros dadayi															+																
Chaetoceros decipiens										+									+					+	+	+	+				+
Chaetoceros didymus																															
Chaetoceros lacinosus															+					+											
Chaetoceros peruvianus																															
Chaetoceros tetrastichon																															
Climacodium frauenfeldianum																															
Coccolithophorids																									+						

Species	32 29°59.3'N 128°34.0'W	33 30°02.9'N 131°12.7'W	34 30°01.9'N 133°52.3'W	35 30°05.7'N 139°05.0'W	36 27°24.0'N 143°54.5'W	37 24°33.0'N 143°53.0'W	38 25°01.6'N 142°10.0'W	39 25°02.1'N 139°46.5'W	40 24°59.7'N 137°19.0'W	41 24°57.3'N 134°49.3'W	42 24°55.9'N 132°17.0'W	43 25°55.9'N 129°57.6'W	44 25°00.9'N 127°36.0'W	45 25°02.8'N 125°10.7'W	46 24°56.7'N 122°36.2'W	47 24°56.0'N 120°09.3'W	48 24°58.8'N 117°49.9'W	49 24°59.5'N 115°21.8'W	50 24°57.9'N 113°25.2'W	51 19°59.1'N 109°03.7'W	52 20°00.0'N 110°02.1'W	53 20°00.9'N 111°57.0'W	54 20°02.1'N 113°56.9'W	55 20°04.3'N 115°51.7'W	56 20°05.6'N 117°47.1'W	57 19°50.3'N 120°16.0'W	58 20°01.3'N 121°59.6'W	59 20°01.8'N 124°02.3'W	60 20°00.2'N 126°02.8'W	61 19°57.7'N 127°58.6'W	62 20°00.0'N 130°01.2'W
Amphisolenia bidentata	+	+	+		+	+		+	+	+		+	+			+			+	+	+	+	+	+			+	+	+	+	+
Amphisolenia rectangulata																															
Amphisolenia spinulosa																							+								
Amphisolenia trinax	+							+	+		+																	+	+		+
Amphisolenia zimmermanni																															
Amphisolenia sp.	+																														
Asterolampa marylandica	+	+	+							+	+	+	+	+		+	+		+		+	+	+		+	+	+				+
Asteromphalus sp.																		+													
Bacteriastrum delicatulum																															
Ceratium arietinum f. detortum																															
Ceratium belose																								+			+	+		+	
Ceratium buceros																															
Ceratium candelabrum			+													+											+				
Ceratium carriense		+																	+								+				
Ceratium contortum										+	+	+	+	+		+	+	+	+	+	+		+		+				+		+
Ceratium declinatum	+							+																+	+						
Ceratium deflexum						+					+	+		+		+		+		+	+	+		+	+		+		+	+	
Ceratium extensum	+	+	+							+	+		+	+		+	+			+	+		+	+	+		+		+		+
Ceratium euarcuatum																															
Ceratium falcatum																															
Ceratium fusus	+							+	+	+								+	+		+		+		+						
Ceratium fusus var. seta																															
Ceratium gravidum	+									+				+			+	+	+		+	+		+	+	+			+		
Ceratium hexacantum f. contortum	+	+		+								+		+			+		+				+	+			+	+	+		
Ceratium hexacantum f. spirale																			+						+						+
Ceratium inflatum												+		+								+	+				+				
Ceratium karstenii												+																			
Ceratium longinum	+			+	+			+											+			+									
Ceratium longirostrum		+						+	+													+									
Ceratium lumula																									+						
Ceratium macroceros								+								+	+	+		+	+				+						+
Ceratium macroceros var. gallicum								+	+	+			+						+												
Ceratium massiliense	+		+	+		+			+	+		+	+	+		+	+			+	+	+	+	+	+	+		+	+	+	
Ceratium pentagonum																															
Ceratium pulchellum												+		+							+										
Ceratium ranipes	+																														
Ceratium trichoceros	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+		+	+	+		+
Ceratium vultus	+	+	+							+			+			+		+	+					+							
Ceratocorys horrida		+	+						+	+			+			+	+	+	+		+	+			+			+			
Chaetoceros affinis																	+			+						+					
Chaetoceros coarctatus		+	+		+	+	+	+	+	+	+	+	+	+		+	+	+			+	+	+	+			+		+		+
Chaetoceros concaviformis																															
Chaetoceros convolutus																															
Chaetoceros dadayi																															
Chaetoceros decipiens					+									+				+													
Chaetoceros didymus																															
Chaetoceros lacinosus		+																													
Chaetoceros peruvianus														+		+															
Chaetoceros tetrastichon																															
Climacodium frauenfeldianum																															
Coccolithophorids																															

Species	63 20°00.0'N 131°59.4'W	64 19°59.9'N 136°01.3'W	65 19°58.6'N 143°58.1'W	66 19°59.2'N 146°00.0'W	67 20°02.0'N 147°58.4'W	68 20°04.5'N 150°00.6'W	69 20°03.0'N 151°49.1'W	70 20°00.8'N 159°01.0'W	71 29°01.9'N 161°03.0'W	72 20°02.2'N 162°05.4'W	73 20°02.6'N 164°09.3'W	74 20°03.4'N 166°11.5'W	75 20°04.8'N 168°06.6'W	76 19°57.8'N 169°59.3'W	77 20°05.2'N 173°33.1'W	78 21°59.5'N 173°36.1'W	79 23°59.1'N 173°37.0'W	80 23°59.2'N 175°03.1'W	81 24°01.9'N 177°02.9'W	82 24°03.8'N 178°56.1'W	83 24°03.1'N 179°01.4'E	84 24°01.5'N 177°04.0'E	85 23°59.6'N 175°00.1'E	86 24°00.2'N 173°00.3'E	87 23°48.2'N 171°00.5'E	88 24°01.4'N 169°01.3'W	89 24°01.6'N 167°23.1'E	90 24°01.3'N 164°56.0'E	91 24°01.8'N 163°02.5'E	92 25°00.5'N 153°59.6'E	93 33°48.5'N 151°19.4'E
Amphisolenia bidentata	+		+	+	+		+		+	+		+	+	+			+	+		+	+	+	+	+	+	+	+	+	+		
Amphisolenia rectangulata																					+							+	+		
Amphisolenia spinulosa																															
Amphisolenia trinax		+				+								+					+		+			+		+					
Amphisolenia zimmermanni																										+					
Amphisolenia sp.																			+												
Asterolampa marylandica	+													+								+	+	+				+	+		
Asteromphalus sp.																															
Bacteriastrum delicatulum																															
Ceratium arietinum f. detortum																															
Ceratium belose	+																				+										
Ceratium buceros																		+		+				+		+			+		
Ceratium candelabrum																															
Ceratium carriense								+	+					+										+							
Ceratium contortum	+	+					+	+		+	+	+	+		+	+			+		+	+		+	+	+		+			
Ceratium declinatum																															
Ceratium deflexum	+	+	+		+			+				+		+	+	+		+	+	+		+	+		+	+	+	+			
Ceratium extensum	+	+		+							+			+			+	+	+			+	+		+	+		+			
Ceratium euarcuatum																					+										
Ceratium falcatum	+														+						+						+		+		
Ceratium fusus	+																									+		+	+	+	
Ceratium fusus var. seta																															
Ceratium gravidum			+			+														+											
Ceratium hexacantum f. contortum	+		+		+									+	+					+	+				+	+			+		
Ceratium hexacantum f. spirale																													+		
Ceratium inflatum				+														+								+					
Ceratium karstenii																															
Ceratium longinum																															
Ceratium longirostrum	+	+																													
Ceratium lumula					+																										
Ceratium macroceros																						+			+				+		
Ceratium macroceros var. gallicum	+											+		+								+	+			+			+		
Ceratium massiliense		+	+			+		+	+		+	+		+	+		+			+	+		+		+		+		+		
Ceratium pentagonum																															
Ceratium pulchellum														+			+														
Ceratium ranipes																									+						
Ceratium trichoceros	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
Ceratium vultus		+					+	+				+		+						+					+	+		+	+		
Ceratocorys horrida	+	+	+		+			+				+					+		+		+	+	+	+	+			+	+	+	
Chaetoceros affinis																															
Chaetoceros coarctatus	+	+	+	+	+	+	+			+	+	+	+	+		+		+	+		+	+	+	+	+	+		+			
Chaetoceros concaviformis																															
Chaetoceros convolutus																															
Chaetoceros dadayi																															
Chaetoceros decipiens																															
Chaetoceros didymus																		+			+		+	+							
Chaetoceros lacinosus																							+								
Chaetoceros peruvianus																															
Chaetoceros tetrastichon																															
Climacodium frauenfeldianum																		+													
Coccolithophorids							+			+		+		+																	

TABLE 5 — PHYTOPLANKTON OF THE EASTERN PACIFIC

B. 19 to 40°N

Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Latitude	40°24.1'N	39°26.9'N	37°48.8'N	36°28.7'N	35°00.0'N	34°59.8'N	34°59.4'N	35°01.6'N	34°58.4'N	40°00.3'N	40°01.0'N	40°01.4'N	40°03.0'N	40°03.0'N	40°20.0'N	40°03.5'N	49°04.9'N	37°35.1'N	36°06.3'N	35°06.8'N	35°00.2'N	34°59.8'N	34°5.4'N	34°57.0'N	34°53.1'N	34°58.3'N	35°02.3'N	30°00.0'N	29°58.4'N	30°00.8'N	30°00.0'N
Longitude	175°41.8'W	176°02.4'W	175°56.9'W	175°57.5'W	176°00.4'W	172°56.5'W	169°37.1'W	166°27.7'W	163°05.4'W	125°08.4'W	127°39.0'W	129°16.0'W	131°26.7'W	133°36.0'W	135°46.9'W	137°54.4'W	140°01.9'W	139°59.7'W	139°58.8'W	137°53.0'W	136°01.7'W	134°01.8'W	132°02.0'W	130°00.0'W	126°01.4'W		121°43.5'W	118°02.6'W	120°43.0'W	123°14.6'W	125°54.0'W
Coscinodiscus asteromphalus																															
Coscinodiscus centralis																											+	+			
Coscinodiscus concinnus																															
Coscinodiscus curvulatus							+																								
Coscinodiscus oculus-iridis																															
Denticula marina								+																							
Dinophysis acuta																+															
Dinophysistripos																										+					
Ditylum brightwellii																															
Ethmodiscus rex						+		+			+			+				+	+	+	+	+	+	+					+	+	+
Goniaulax polyedra																												+			
Gossleriella sp.																		+			+						+				
Guinardia flaccida																															+
Halosphaera viridis																														+	
Halosphaera sp.								+											+		+	+	+	+							
Hemiaulus hauckii																			+	+								+	+	+	
Hemiaulus sinensis																															
Nitzschia seriata										+																					
Ornithoceros stenii																															
Oscillatoria thiebautii	+	+					+		+	+	+	+		+	+		+	+	+		+			+		+		+	+	+	+
Peridinium elegans																															
Peridinium fatulipes																															
Peridinium leonis																									+						
Planktoniella sol										+																	+	+			
Prorocentrum micans																															
Pseudoeunotia doliolus														+																	
Pyrocystis acuta																															+
Pyrocystis fusiformis						+			+									+	+	+	+	+	+	+					+	+	
Pyrocystis hamulus																															
Pyrocystis lanceolata																															
Pyrocystis pseudonoctiluca		+	+		+	+	+	+	+	+				+		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+
Rhizosolenia acuminata																						+					+			+	
Rhizosolenia alata										+	+		+												+						
Rhizosolenia bergonii																															
Rhizosolenia calcar-avis								+											+					+		+	+		+		
Rhizosolenia castracanei				+				+													+	+		+						+	+
Rhizosolenia hebetata													+																		
Rhizosolenia hebetata f. semispina						+		+		+	+	+			+		+	+	+	+	+	+		+	+		+			+	+
Rhizosolenia macroceros																															
Rhizosolenia robusta										+														+		+	+				+
Rhizosolenia styliformis																			+	+	+	+		+	+					+	+
Skeletonema costatum	+				+	+	+		+																						
Stephanopyxis turris																												+			
Surirella fatuosa var. recedens																															
Thalassionema nitzschoides						+																				+					
Thalassiothrix delicatula									+																	+	+	+			
Thalassiothrix frauenfeldianum																										+		+			
Thalassiothrix longissima				+	+					+		+														+				+	+

Station	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
Latitude	29°59.3'N	30°02.9'N	30°01.9'N	30°05.7'N	27°24.0'N	24°33.0'N	25°01.6'N	25°02.1'N	24°59.7'N	24°57.3'N	24°55.9'N	25°55.9'N	25°00.9'N	25°02.8'N	24°56.7'N	24°56.0'N	24°58.8'N	24°59.5'N	24°57.9'N	19°59.1'N	20°00.0'N	20°00.9'N	20°02.1'N	20°04.3'N	20°05.6'N	19°50.3'N	20°01.3'N	20°01.8'N	20°00.2'N	19°57.7'N	20°00.0'N
Longitude	128°34.0'W	131°12.7'W	133°52.3'W	139°05.6'W	143°54.5'W	143°53.8'W	142°10.0'W	139°46.5'W	137°19.0'W	134°49.3'W	132°17.0'W	129°57.6'W	127°36.0'W	125°10.7'W	122°36.2'W	120°09.3'W	117°49.9'W	115°21.8'W	113°25.2'W	109°03.7'W	110°02.1'W	111°57.0'W	113°56.9'W	115°51.7'W	117°47.1'W	120°16.0'W	121°59.6'W	124°02.3'W	126°02.8'W	127°58.6'W	130°01.2'W
Coscinodiscus asteromphalus																										+					
Coscinodiscus centralis																															
Coscinodiscus concinnus																							+	+		+			+		
Coscinodiscus curvulatus																															
Coscinodiscus oculus-iridis																									+	+					
Denticula marina																															
Dinophysis acuta																															
Dinophysistripos				+																											
Ditylum brightwellii					+																										
Ethmodiscus rex	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+		+	+	+	+	+	+
Goniaulax polyedra																															
Gossleriella sp.								+								+		+	+												
Guinardia flaccida																															
Halosphaera viridis													+			+				+											
Halosphaera sp.	+								+	+		+		+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+
Hemiaulus hauckii		+	+		+	+	+	+	+	+	+	+	+	+																	
Hemiaulus sinensis																															
Nitzschia seriata																															
Ornithoceros stenii		+																				+					+				
Oscillatoria thiebautii		+						+				+	+						+		+		+							+	+
Peridinium elegans																+															
Peridinium fatulipes																+															
Peridinium leonis																															
Planktoniella sol																	+	+	+	+	+	+	+	+	+	+	+				
Prorocentrum micans				+																											
Pseudoeunotia doliolus																															
Pyrocystis acuta	+		+								+																				
Pyrocystis fusiformis	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+
Pyrocystis hamulus																		+			+	+									+
Pyrocystis lanceolata		+					+			+	+	+	+																		+
Pyrocystis pseudonoctiluca	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Rhizosolenia acuminata													+			+								+	+		+				
Rhizosolenia alata																							+	+					+		+
Rhizosolenia bergonii		+																+	+		+								+		
Rhizosolenia calcar-avis			+		+		+					+		+							+										
Rhizosolenia castracanei	+	+	+		+		+	+	+	+	+	+	+	+			+	+	+		+	+	+	+	+		+		+	+	+
Rhizosolenia hebetata																													+		
Rhizosolenia hebetata f. semispina	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+					+	+			+				+
Rhizosolenia macroceros																															
Rhizosolenia robusta																+	+	+													
Rhizosolenia styliformis	+	+	+			+	+	+	+			+	+	+							+	+	+				+				
Skeletonema costatum																															
Stephanopyxis turris																															
Surirella fatuosa var. recedens																			+												
Thalassionema nitzschoides																		+													
Thalassiothrix delicatula																			+				+								
Thalassiothrix frauenfeldianum																								+							
Thalassiothrix longissima	+	+	+		+					+		+	+			+	+	+		+	+	+	+	+			+	+	+		

Station	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
Latitude	20°00.0'N	19°59.9'N	19°58.6'N	19°59.2'N	20°02.0'N	20°04.5'N	20°03.0'N	20°00.8'N	29°01.0'N	20°02.6'N	20°02.6'N	20°03.4'N	20°04.8'N	19°57.8'N	20°05.2'N	21°59.5'N	23°59.1'N	23°59.2'N	24°01.9'N	24°03.8'N	24°03.1'N	24°01.5'N	23°59.6'N	24°00.2'N	23°48.2'N	24°01.4'N	24°01.6'N	24°01.3'N	24°01.8'N	25°00.0'N	33°48.5'N
Longitude	131°59.4'W	136°01.3'W	143°58.1'W	146°00.0'W	147°58.4'W	150°00.6'W	151°49.1'W	159°01.0'W	161°03.9'W	162°05.4'W	164°09.3'W	166°11.5'W	168°06.6'W	169°59.3'W	173°33.1'W	173°36.1'W	173°37.0'W	175°03.1'W	177°02.9'W	178°56.1'W	179°01.4'E	177°04.0'E	175°00.1'E	173°00.2'E	171°00.5'E	169°01.3'E	167°23.1'E	164°56.0'E	163°02.5'E	153°59.6'E	151°19.4'E
Coscinodiscus asteromphalus																															
Coscinodiscus centralis																															
Coscinodiscus concinnus																															
Coscinodiscus curvulatus																															
Coscinodiscus oculus-iridis																															
Denticula marina																															
Dinophysis acuta																															
Dinophysistripos																															
Ditylum brightwellii																															
Ethmodiscus rex	+	+	+	+	+		+	+				+	+	+	+	+			+	+	+	+	+	+			+		+	+	+
Goniaulax polyedra																															
Gossleriella sp.											+	+		+				+	+			+	+	+							
Guinardia flaccida																															
Halosphaera viridis													+										+				+				
Halosphaera sp.		+		+	+	+				+				+		+	+		+		+				+		+			+	
Hemiaulus hauckii								+		+	+	+	+	+								+	+		+	+	+	+	+		
Hemiaulus sinensis											+																				
Nitzschia seriata																															
Ornithoceros stenii																												+	+		
Oscillatoria thiebautii	+				+			+	+		+	+		+		+	+	+	+		+	+		+	+		+	+	+		
Peridinium elegans												+		+															+		
Peridinium fatulipes																									+						
Peridinium leonis																															
Planktoniella sol	+											+			+					+		+		+		+					
Prorocentrum micans																															
Pseudoeunotia doliolus																															
Pyrocystis acuta														+	+							+			+			+			
Pyrocystis fusiformis	+	+	+	+	+	+	+	+	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+
Pyrocystis hamulus	+			+			+	+		+				+		+		+	+	+		+		+	+		+	+	+	+	
Pyrocystis lanceolata	+	+																					+	+	+						
Pyrocystis pseudonoctiluca	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+		+	+	+	+	+
Rhizosolenia acuminata							+												+												
Rhizosolenia alata																							+	+							
Rhizosolenia bergonii																			+										+		
Rhizosolenia calcar-avis							+	+	+			+	+					+	+		+		+	+		+		+			
Rhizosolenia castracanei		+		+	+	+	+	+	+	+		+		+				+	+		+	+	+	+		+	+	+	+		
Rhizosolenia hebetata											+																				
Rhizosolenia hebetata f. semispina	+	+	+		+		+	+				+	+	+	+	+		+	+			+	+	+	+	+	+	+	+		
Rhizosolenia macroceros	+																														
Rhizosolenia robusta																															
Rhizosolenia styliformis					+							+																	+		
Skeletonema costatum																															
Stephanopyxis turris																															
Surirella fatuosa var. recedens																															
Thalassionema nitzschoides																															
Thalassiothrix delicatula										+			+									+									
Thalassiothrix frauenfeldianum																															
Thalassiothrix longissima	+	+										+							+			+	+								

TABLE 6 — Phytoplankton of the Equatorial Pacific

BACCILARIOPHYCEAE	
Centrales	
Actinocyclus ehrenbergii	Coscinosira oestrupii
Actinocyclus sp.	Dactyliosolen mediterraneum
Asteromphalus flabellatus	Planktoniella sol
Bacteriastrum elegans	Rhizosolenia alata
Brenneckella lorenzenii	Rhizosolenia bergonii
Chaetoceros aequatorialis	Rhizosolenia cylindrus
Chaetoceros atlanticus var. neapolitanus	Rhizosolenia styliformis
Chaetoceros peruvianus	Thalassiosira antarctica
Chaetoceros cf. socialis	Thalassiosira decipiens
Chaetoceros tetrastichon	Thalassiosira sp.
Coscinodiscus crenulatus	Triceratium cf. formosum
Coscinodiscus excentricum	Triceratium sp.
Pennales	
Asterionella sp.	Thalassionema elegans
Nitzschia bicapitata	Thalassionema nitzchoides var. inflata
Nitzschia cf. closterium	Thalassionema nitzchoides var. parva
Nitzschia delicatissima	Thalassiothrix cf. delicatula
Nitzschia kolaizeckii	Thalassiothrix cf. frauenfeldii
Nitzschia pacifica	Thalassiothrix cf. vanhoeffenii
Nitzschia sicula	Thalassiothrix sp.
Nitzschia sp.	Tropidoneis sp. 1
Pseudoeunotia dololus	Tropidoneis sp. 2
COCCOLITHOPHORIDACEAE	
Acanthoica quattrospina	Ophiaster sp.
Anoplosolenia sp.	Pontosphaera discopora (?)
Anthosphaera sp.	Pontosphaera nana
Calciosolenia sp.	Pontosphaera sessilis
Calciopappus (?) sp.	Rhabdosphaera erinaceus
Calyptrosphaera cf. quadridentata	Rhabdosphaera stylifer
Coccolithus huxleyi	Rhabdosphaera cf. tignifer
Cyclococcolithus fragilis	Syracosphaera mediterranea
Cyclococcolithus leptoporus	Syracosphaera molischii
Cyclococcolithus mirabilis	Syracosphaera pulchra
Cyclococcolithus sibogae	Syracosphaera tuberculata
Deutschlandia sp.	Syracosphaera sp. 1
Gephyrocapsa sp.	Syracosphaera sp. 2
Halopappus sp.	Thoracosphaera heimii
Helicosphaera carterii	Thorosphaera flabellata
Lohmannosphaera sp.	Umbellosphaera irregularis
Michaelsarsia sp.	
OTHER FLAGELLATES, etc.	
Chilomonas marina	"Olivgrüne Zellen"
Danasphaera indica	Peranema sp.
Dictyocha fibula var. messanenesis	Pterosperma cristatum
Halosphaera viridis	Pterosperma parallelum
Monosiga marina	Solenicola setigera

Hasle, Grethe Rytter. Deep Sea Research 6, 38-59 (1959).

TABLE 7 — Phytoplankton of the Northwestern Pacific Ocean

Type of water	No. of species recorded	Representative species
Cold water (chiefly arctic region)	10	Ceratium arcticum Rhizosolenia alata f. curvirostris Rhizosolenia hebetata f. hiemalis
Temperate cold water (chiefly northern part of boreal region)	27	Ceratium fusus Ceratium longipes Chaetoceros atlanticus Chaetoceros concavicornis Thalassiosira nordenskiöldii
Temperate warm water (chiefly southern part of boreal region)	19	Ceratium tripos Ceratium macrosceros Chaetoceros affinis Chaetoceros convolutus Thalassiosira subtilis
Warm water (tropical region)	55	Ceratium extensum Ceratium massiliense Ceratocorys armata Ceratocorys horrida Chaetoceros coarctatus Chaetoceros lorenzianus Chaetoceros peruvianus Chaetoceros messanensis Climadocium biconcavum Ethmodiscus rex Pyrecystis pseudonoctiluca Pyrecystis fusiformis Pyrecystis hamulus Rhizosolenia bergonii Trichodesmium thiebauti

L. I. Smirnova, Doklady Akad. Nauk SSSR 109, 649-652 (1956).
B. G. Bogorov, Deep Sea Res. 5, 149-161 (1958).

TABLE 8— Plankton Diatoms Around Japan

Asterionella japonica	Climacodium biconcavum
Bacteriastrum varians	Climacodium frauenfeldianum
Bacteriastrum elongatum	Coscinodiscus granii
Bacteriastrum comosum	Coscinodiscus wailesii
Biddulphia sinensis	Coscinodiscus spp.
Chaetoceros eibenii	Corethron hystrix
Chaetoceros coarctatus	Ditylum brightwellii
Chaetoceros decipiens	Eucampia zoodiacus
Chaetoceros lorenzianus	Melosira nummuloides
Chaetoceros compressus	Nitzschia seriata
Chaetoceros didymus	Hemidiscus cuneiformis
Chaetoceros affinis	Rhizosolenia alata
Chaetoceros distans	Rhizosolenia stolterfothii
Chaetoceros messanensis	Skeletonema costatum
Chaetoceros curvisetus	Stephanopyxis palmeriana
Chaetoceros pseudocurvisetus	Synedra spp.
Chaetoceros radicans	Thalassionema nitzschioides
Chaetoceros socialis	Thalassiosira spp.
	Thalassiothrix frauenfeldii

K. Karohji, Bull. Fac. Fish. Hokkaido Univ. 7, 271-283 (1957).

TABLE 9— Phytoplankton of New Zealand Waters

DIATOMS	
Asterionella japonica	Melosira granulata
Asterionella gracilina	Nitzschia closterium
Biddulphia chinensis	Nitzschia seriata
Chaetoceros armatun (?)	Rhizosolenia setigera
Chaetoceros sociale	Rhizosolenia styliformis
Corethron criophilum	Synedra fulgeus
Coscinodiscus centralis	Thalassiosira condensata
Coscinodiscus concinnus	Thalassiosira decipiens
Coscinodiscus marginatus	Thalassiosira hyalina
Coscinodiscus oculus iridis	Thalassiosira rotula
Coscinodiscus wailesii	Thalassiothrix nitzschoides
Dinobryon divergens	
DINOFLAGELLATES	
Ceratium arietinum	Exuviaella marina
Ceratium furca	Peridinium pedunculatum
Ceratium fusus	Peridinium pellucidum
Ceratium tripos	Phalacroma ovum
Dinophysis fortii	Prorocentrum micans

R. M. Cassie, N. Z. Journ. of Sci. 3, 26-50 (1960).
V. Cassie, N. Z. Journ. of Sci. 3, 137-162 (1960).

TABLE 10 — Phytoplankton Between New Zealand and Fiji

MYXOPHYCEAE

Anacystis montana f. minor
Oscillatoria thiebautii
Katagnymene spiralis
Richelia intracellularis

CHLOROPHYCEAE

Pseudotetraspora marina

XANTHOPHYCEAE

Halosphaera viridis
Asterogloea undicola

CHRYSOPHYCEAE

Tetrasporopsis pelagica
Chrysochromulina spp.
Dictyocha fibula
Coccolithophorineae
- Acanthoica acanthifera
- Acanthoica quattrospina
- Acanthosolenia mediterranea
- Anoplosolenia brasiliensis
- Anthosphaera robusta
- Calcidiscus quadriforatus
- Calyptrosphaera insignis
- Coccolithus huxleyi
- Corisphaera fagei
- Scyphosphaera apsteini
- Syracosphaera binodata
- Syracosphaera corii
- Syracosphaera dalmatica
- Syracosphaera histrica

Coccolithophorineae (cont'd)
- Cyclococcolithus leptoporus
- Discosphaera tubifer
- Gephyrocapsa oceanica
- Helicosphaera carteri
- Lohmannosphaera paucoscyphos
- Michaelsarsia splendens
- Ophiaster hydroideus
- Pontosphaera caelamensis
- Pontosphaera granii
- Pontosphaera syracusana
- Rhabdosphaera claviger
- Rhabdosphaera stylifer
- Syracosphaera mediterranea
- Syracosphaera molischi
- Syracosphaera pulchra
- Thoracosphaera heimi
- Umbellosphaera irregularis

EUGLENOPHYCEAE

Euglenopsis zabra

DINOPHYCEAE

Protapsis tanyopsis
Amphidinium acutum
Amphidinium aloxalocium
Amphidinium lacustriforme
Amphidinium microcephalum
Gymnodinium cassiei
Gymnodinium diamphidinium
Gymnodinium exechegloutum
Gymnodinium grammaticum
Gymnodinium leptum
Gymnodinium minor
Gymnodinium simplex
Gyrodinium apidiomorphum
Gyrodinium chiasmonetrium
Gyrodinium kofoidii
Gyrodinium phorkorium
Paulsenella chaetoceratis

CRYPTOPHYCEAE

Chilomonas marina

R. E. Norris, N. Z. Journal of Sci. 4, 162-188 (1961).

TABLE 11 — Australia and New Zealand Phytoplankton

I. DIATOMS

Actinocyclus octonavius
Asteromphalus elegans
Ausliscus punctatus
Bacteriastrum comosum
Bacteriastrum delicatulum[1,6]
Bacteriastrum hyalinum
Bacteriastrum varians
Bellerochea malleus
Biddulphia aurita
Biddulphia chinensis
Biddulphia cylindrata
Biddulphia mobiliensis[1]
Biddulpha pulchella
Biddulphia reticulata
Biddulphia thunii
Cerataulina chapmanii
Charcotia bifrons
Chaetoceros affine[2]
Chaetoceros atlanticum
Chaetoceros boreale
Chaetoceros castracanei
Chaetoceros cinctum
Chaetoceros coarctatum[1]
Chaetoceros simplex
Chaetoceros sociale
Chaetoceros vanheureckii
Chaetoceros vistulae
Climacodium frauenfeldianum[1]
Corethron criophilum
Coscinodiscus centralis
Coscinodiscus excentricus
Coscinodiscus gazellae
Coscinodiscus gigas
Coscinodiscus granii
Coscinodiscus granulosus
Coscinodiscus janischii
Coscinodiscus marginalis
Coscinodiscus oculus iridis
Coscinodiscus rex
Coscinodiscus strigillatus
Dactyliosolen mediterraneum
Dactyliosolen antarcticum
Detonula confervacea[1]
Ditylum brightwellii
Ditylum sol
Eucampia zoodiacus
Eucampia balaustium
Gossleriella punctata
Gossleriella tropica
Rhizosolenia setigera
Rhizosolenia stolterforthii
Rhizosolenia styliformis[1,4,6]
Rhizosolenia styliformis f. latissima[4]
Schroderella delicatula
Skeletonema costatum
Stephanopyxis orbicularis
Stephanopyxis palmeriana[1]
Stephanopyxis turris[2]
Stictodiscus argus
Chaetoceros compressum[2]
Chaetoceros concaviforme[3]
Chaetoceros convolutum[2,4]
Chaetoceros criophilum
Chaetoceros danicum
Chaetoceros debile[1]
Chaetoceros decipiens
Chaetoceros denticulatum
Chaetoceros dichaeta[2]
Chaetoceros didymum[2,6]
Chaetoceros difficile
Chaetoceros diversum
Chaetoceros eibenii[6]
Chaetoceros laciniosum
Chaetoceros laeve
Chaetoceros lauderii
Chaetoceros lorenzianum
Chaetoceros messanense[4]
Chaetoceros mitra[2]
Chaetoceros paradoxum
Chaetoceros pendulum
Chaetoceros peruvianum
Chaetoceros simile
Guinardia flaccida
Hemiaulus hauckii[1]
Hemidiscus cunieformis
Hyalodiscus purtulatus
Hyalodiscus stelliger
Isthmia nervosa
Isthmia enervis
Lauderia annulata
Melosira granulata
Melosira moniloformis
Planktoniella florea
Planktoniella sol
Rhizosolenia alata[6]
Rhizosolenia acuminata
Rhizosolenia bergonii[5]
Rhizosolenia calcar-avis[1,6]
Rhizosolenia castracanei[1,5]
Rhizosolenia chunii
Rhizosolenia clevei[1]
Rhizosolenia curvata
Rhizosolenia cylindrica[2]
Rhizosolenia delicatula
Rhizosolenia hebetata
Rhizosolenia hebetata f. hiemalis[3]
Rhizosolenia imbricata
Rhizosolenia robusta[1,4]
Streptotheca thamesis[1]
Thalassiosira baltica[2]
Thalassiosira condensata[2]
Thalassiosira decipiens
Thalassiosira rotula[2]
Thalassiosira subtilis[2]
Triceratium alternans
Triceratium arcticum
Triceratium favus
Triceratium pentacrinum

TABLE 11 — Continued

I. DIATOMS — Continued

Streptotheca indica[1]
Triceratium reticulum

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1. Indicator species for Coral Sea Water Mass.
2. Indicator species for East Australian Current.
3. Characteristic cool temperate species of Tasmania and Bass Strait.
4. Indicator species of West Wind Drift.
5. Characteristic species of South Australian Gulf.
6. Indicator species of tropical Indian Ocean water.

L. H. Crosby and E. J. Ferguson Wood, Trans. Roy. Soc. N.Z. 85, 483-530 (1958).
E. J. Ferguson Wood, L. H. Crosby, and V. M. Cassie, ibid. 87, 211-219 (1959).

II. DINOFLAGELLATES

Amphidinium inflatum
Amphidinium kesslitzi
Amphidinium klebsi
Amphidinium sulcatum
Amphisolenia bidentata
Amphisolenia bisponosa
Amphisolenia curvata
Amphisolenia palmata
Amphisolenia thrinax
Centrodinium sp.
Ceratium arietinum
Ceratium axiale
Ceratium azoricum[4]
Ceratium belone
Ceratium breve
Ceratium bucephalum
Ceratium buceros
Ceratium buceros f. claviger
Ceratium buceros f. denticulatum
Ceratium buceros f. inclinatum
Ceratium buceros f. leptosomum
Ceratium buceros f. molle
Ceratium buceros f. tenue
Ceratium buceros f. tenuissimum
Ceratium candelabrum
Ceratium candelabrum f. commune
Ceratium gibberum
Ceratium gibberum f. subaequale
Ceratium gravidum[4]
Ceratium hexacanthum
Ceratium hirundinella
Ceratium horridum[2]
Ceratium humile
Ceratium incisum
Ceratium inflatum
Ceratium karstenii
Ceratium kofoidii[5]
Ceratium limulus
Ceratium lineatum
Ceratium longinum
Ceratium longipes
Ceratium longipes f. balticum
Ceratium longirostrum
Ceratium longissimum
Ceratium candelabrum f. curvatulum
Ceratium candelabrum f. depressum
Ceratium carriense
Ceratium carriense f. ceylanicum
Ceratium carriense f. hundhausenii
Ceratium carriense f. volans
Ceratium cephalotum[5]
Ceratium compressum?
Ceratium concilians
Ceratium contortum
Ceratium contortum f. subcontortum
Ceratium declinatum
Ceratium deflexum
Ceratium dens
Ceratium euarcuatum
Ceratium extensum
Ceratium extensum f. strictum
Ceratium falcätiforme[4]
Ceratium falcatum
Ceratium furca
Ceratium furca var. berghii
Ceratium furca var. eugrammum
Ceratium fusus
Ceratium fusus var. schütii
Ceratium fusus var. seta
Ceratium geniculatum
Ceratium minutum
Ceratium paradoxides
Ceratium pavillardii[4]
Ceratium pentagonum
Ceratium petersii[3]
Ceratium platycorne[4]
Ceratium porrectum
Ceratium pulchellum
Ceratium pulchellum f. semipulchellum
Ceratium ranipes
Ceratium reflexum
Ceratium schmidtii[5]
Ceratium setaceum[5]
Ceratium symmetricum
Ceratium teres
Ceratium trichoceros
Ceratium trichoceros f. claviceps
Ceratium trichoceros var. contrarium

TABLE 11—Continued

II. DINOFLAGELLATES—Continued

Ceratium lunula
Ceratium macroceros
Ceratium macroceros subsp. gallicum
Ceratium massiliense
Ceratium massiliense f. armatum
Ceratium massiliense f. macroceroides
Ceratium massiliense f. protuberans
Ceratocorys armata
Ceratocorys gourreti
Ceratocorys horrida
Cochlodinium archimedes
Cochlodinium helix
Dinophysis acuminata
Dinophysis acuta
Dinophysis arctica[1]
Dinophysis caudata
Dinophysis caudata var. diegensis
Dinophysis fortii[4]
Dinophysis hastata
Dinophysis miles
Dinophysis okamurai
Dinophysis ovum
Dinophysis sacculus
Dinophysis schroederi
Dinophysis similis
Dinophysis sphaerica
Dinophysis tripos
Dinophysis truncata[3]
Dinophysis tuberculata[1]
Dinophysis uracantha
Diplopsalis lenticula
Diplopsalis lenticula f. minor
Goniodoma sphaericum
Hemidinium nasutum
Heterodinium asymmetricum
Heterodinium blackmani
Heterodinium dispar
Heterodinium doma
Heterodinium scrippsi
Histioneis carinata
Histioneis depressa
Histioneis dolon
Histioneis hippoperoides
Noctiluca miliaris
Ornithocercus biclavatus
Ornithocercus carolinae
Ornithocercus heteroporus
Ornithocercus magnificus
Ornithocercus quadratus
Ornithocercus splendidus
Ornithocercus steinii[5]
Ornithocercus thurni
Ornithocercus triclavatus
Oxyrrhis marina
Oxytoxum diploconus
Oxytoxum gigas
Oxytoxum scolopax
Ceratium tripos
Ceratium tripos var. atlanticum
Ceratium tripos f. balticum
Ceratium tripos f. tripodioides
Ceratium vultur
Ceratium vultur f. japonicum[5]
Ceratium vultur f. sumatranum[5]
Diplopsalis orbicularis
Diplopsalis rotundata
Exuviaella compressa
Exuviaella marina
Goniaulax alaskensis
Goniaulax apiculata
Goniaulax birostris
Goniaulax conjuncta
Goniaulax diacantha
Goniaulax diegensis
Goniaulax digitale
Goniaulax fragilis
Goniaulax glyptorhynchus
Goniaulax hyalina
Goniaulax kofoidii
Goniaulax minima
Goniaulax monacantha
Goniaulax pacifica
Goniaulax polyedra
Goniaulax polygramma
Goniaulax scrippsae
Goniaulax sp.
Goniaulax spinifera
Goniaulax turbynei
Goniodoma polyedricum
Oxytoxum sp.
Oxytoxum subulatum
Oxytoxum turbo
Parahistioneis reticulata
Parahistioneis rotundata
Peridinium abei
Peridinium achromaticum
Peridinium africanum
Peridinium ampulliforme
Peridinium breve
Peridinium brevipes
Peridinium brochii[5]
Peridinium brochii f. inflatum
Peridinium centenniale
Peridinium cerasus
Peridinium claudicans
Peridinium conicoides
Peridinium conicum
Peridinium conicum f. asamushi
Peridinium crassipes
Peridinium curtipes
Peridinium curvipes
Peridinium dakariensis
Peridinium decipiens
Peridinium depressum

TABLE 11—Continued

II. DINOFLAGELLATES—Continued

Peridinium diabolus
Peridinium divaricatum
Peridinium divergens
Peridinium elegans[4]
Peridinium excentricum
Peridinium gatunense
Peridinium gatunense var. zonatum
Peridinium globulus[5]
Peridinium grande
Peridinium granii
Peridinium hirobis
Peridinium inconspicuum
Peridinium latispinum[5]
Peridinium latum
Peridinium leonis
Peridinium marielebourae
Peridinium mite
Peridinium monocanthum
Peridinium murrayi
Peridinium nudum
Peridinium oblongum
Peridinium obovatum
Peridinium oceanicum
Peridinium okamurai[5]
Peridinium thorianum
Peridinium turbinatum[1]
Peridinium umbonatum
Peridinium variegatum
Peridinium ventricum
Peridinium volzii
Peridinium volzii var. botanicum
Peridinium volzii f. maendricum
Peridinium wiesneri
Phalacroma acutum
Phalacroma alata
Phalacroma apicatum
Phalacroma argus
Phalacroma cuneus
Phalacroma dolichopterygium
Phalacroma doryphorum
Phalacroma elongatum
Phalacroma favus
Phalacroma hindmarchii
Phalacroma irregulare
Phalacroma jibbonense
Phalacroma lens
Phalacroma mawsonii
Phalacroma minutum
Protoceratium reticulatum
Pseudophalacroma nasutum
Pyrocystis acuta
Pyrocystis fusiformis
Pyrocystis fusiformis f. biconica
Pyrocystis hamulus
Pyrocystis hamulus var. semicircularis
Peridinium ovatum[1]
Peridinium ovum
Peridinium pallidum
Peridinium pedunculatum
Peridinium pellucidum
Peridinium pentagonum
Peridinium pentagonum var. latissimum
Peridinium piriforme
Peridinium punctulatum
Peridinium pusillum
Peridinium quarnerense[5]
Peridinium remotum
Peridinium roseum
Peridinium solidicorne
Peridinium sphaericum
Peridinium steinii
Peridinium steinii var. mediterraneum
Peridinium striolatum
Peridinium striolatum f. acuminatum
Peridinium striolatum f. auburnense
Peridinium striolatum f. rugosum
Peridinium striolatum f. truncatum
Peridinium subinerme
Peridinium tenuissimum
Phalacroma mitra
Phalacroma operculatum
Phalacroma ovum
Phalacroma porosum
Phalacroma pulchellum[3]
Phalacroma pulchrum
Phalacroma rapa
Phalacroma rudgei
Phalacroma thompsonii
Phalacroma triangulare
Phalacroma whiteleggei
Podolampas bipes
Podolampas bipes f. reticulata
Podolampas palmipes
Podolampas sp.
Porella perforata
Pronoctiluca acuta
Pronoctiluca acuta var. curvata
Pronoctiluca pelagica
Pronoctiluca spinifera
Prorocentrum dentatum
Prorocentrum micans
Prorocentrum rostratum
Prorocentrum scutellum
Pyrocystis lunula
Pyrocystis pseudonoctiluca
Pyrocystis robusta[4]
Pyrocystis sp.
Pyrophacus horologicum
Pyrophacus horologicum var. steinii
Spiraulax jollifei

1. Antarctic indicator species
2. Cool temperate species

TABLE 11 — Continued

3. Sub-antarctic indicator species
4. Indicator species of East Australian Current
5. Coral Sea indicator species

E. J. F. Wood, Austr. J. Mar. and Freshw. Res. 5, 171-351 (1954)
E. Steemann-Nielsen, Rep. Exped. "Dana" 1(4), (1934)

TABLE 12 — Phytoplankton in the Peru Coastal Current

Dominant genera between 2° 11′ S. and 35° 40′	
Chaetoceros	Thalassiosira
Coscinodiscus	Thalassiothrix
Corethron	Trichodesmium
Planktoniella	Synedra
Rhizosolenia	

E. R. Gunther, Discovery Repts. 13, 107-276 (1936).

TABLE 13 — Phytoplankton Near New Caledonia

Organism	Station No. 1 A	5 A	11 A	22 A
Diatoms				
Chaetoceros coarctatum	+	+		+
Chaetoceros vanheurckii		+	+	
Hemiaulus hauckii	+	+	+	
Climacodium frauenfeldianum		+	+	+
Asterolampra dallasiana		+		
Thalassiothrix longissima	+	+	+	+
Mastogloia rostrata	+	+	+	
Rhizosolenia hebetata semispina ?	+	+	+	+
Dinoflagellates				
Phalacroma ovum			+	
Ornithocercus steinii		+	+	+
Ornithocercus thurni		+		
Ornithocercus sp. 1		+	+	+
Ornithocercus sp. 2		+	+	
Amphisolenia bidentata	+	+	+	+
Amphisolenia bispinosa		+		
Ceratocorys horrida		+	+	+
Pyrophacus horologicum	+	+	+	+
Pyrocystis pseudonoctiluca	+	+	+	+
Pyrocystis hamulus	+	+		
Pyrocystis fusiformis		+	+	
Peridinium elegans				+
Podolampas spinifer	+			
Podolampas palmipes		+		
Oxytoxum sp.	+			
Ceratium teres	+	+		+
Ceratium setaceum	+	+	+	+
Ceratium extensum	+		+	+
Ceratium contortum	+	+		+
Ceratium incisum	+			
Ceratium trichoceros	+	+	+	+
Ceratium macroceros gallicum		+	+	+
Ceratium longirostrum		+		
Ceratium symmetricum		+		
Ceratium furca		+		
Ceratium buceros		+		+
Ceratium hexacanthum		+		+
Ceratium fusus		+	+	+
Ceratium euarcuatum		+		
Ceratium declinatum		+	+	
Ceratium tripos tripodioides		+		+
Ceratium belone		+		
Ceratium karstenii		+		
Ceratium pentagonum			+	+
Ceratium pulchellum			+	
Ceratium carriense volans			+	+
Ceratium gravidum				+
Ceratium candelabrum				+

Henri Rotschi, Michel Angot, and Roger Desrosieres, Institut Francais d'Océanie, Rapport Scientifique No. 16 (1960).

A REVIEW OF THE RECENT DEVELOPMENT OF TECHNIQUES MEASURING PRIMARY PRODUCTION

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I. INTRODUCTION

Limnologists and marine biologists have for a long time carefully focused their attention on the organic matter production in fresh and marine waters, but dynamic studies on primary production have only been executed in the last decade. The concept of "production," as defined by Thienemann (1931), is the total amount of organic matter produced in a given space during a given period, but it has often been confused with the concept of standing crop.

Most of the early studies on primary production were, with few exceptions, restricted to the indirect estimation of production by long-term changes of the standing crop and the concentration of inorganic nutrients or dissolved gases. Recently, primary production has been determined by the direct measurement of photosynthesis, since the basis of the organic matter production in the water is the photosynthesis of plants, especially of phytoplankton. For this purpose, the so-called "light and dark bottle oxygen method" has usually been employed, but the sensitiveness of this method is unfortunately insufficient in low productive areas. The drawback has been overcome by the radioisotope carbon tracer technique introduced by Steemann-Nielsen (1952). On the other hand, the chlorophyll method has been developed for the determination of the standing crop of phytoplankton. These two methods, together, have brought advancement in the study of matter production in the water.

Considering the foregoing facts, the present paper will give a short review of recent developments of the techniques for measuring primary production. For details of this subject, the following excellent papers are suggested for reference: Ryther (1956b), Gessner (1959), Vinberg (1960), Steemann-Nielsen (1960b) and Strickland (1960).

II. MEASUREMENT OF PRODUCTION FROM THE CHANGE IN STANDING CROP OR IN DISSOLVED SUBSTANCES IN WATER.

The initial attempt to estimate production was made by Lohmann (1908) from the changes in standing crop by taking into account the rate of reproduction, grazing by zooplankton, etc. This method was adopted by limnologists with success. Juday (1940) calculated the annual production and energy utilization at each stage of the food chain in Lake Mendota on the assumption that the plankton life cycle alternates every two weeks. Lindemann (1942) made a similar estimation with more elaborate results in Cedar Bog Lake. However, the results from this approach to production estimation appear to be reliable only when the method is applied to a large aquatic plant community.

Cushing (1955) describes what is known as the "cell-size decrease method." The number of divisions was estimated from the difference in cell number in two successive observations in the sea. But this is only applicable to diatoms in the open sea.

The estimation of production from long term changes of the concentration of inorganic nutrients or dissolved gases has been employed since the early 1920's. Atkins (1922, 1923, and 1924) used changes in CO_2 and later in phosphates in the English Channel. Cooper (1938) used both oxygen and nitrate. Recently, Steele (1956 and 1958) measured the changes of inorganic phosphate in the northern area of the North Sea for estimation of annual production. He found good agreement between the results from this indirect method with phosphate and those from the carbon-14 method. Seiwell (1935), Riley (1946) and Riley and Gorgy (1948) tried to measure production from the data on oxygen decreases in deep layers.

The estimation of production by these methods involves the effect of decomposition, grazing, mixing, sinking, etc. Reliable results, therefore, can be expected to be obtained only when exact information is available as to the effect of the factors concerned.

III. DIRECT MEASUREMENT OF PRODUCTION BASED ON THE DETERMINATION OF PHOTOSYNTHESIS

The direct method can be classified into the following three categories: the pH, oxygen, and carbon-14 methods.

1. pH method: Moore (in Johnstone, Scott and Chadwick, 1924) calculated the production on the basis of pH change which is caused in water by the uptake and release of carbon dioxide through photosynthesis and respiration. Verduin (1951, 1956a, and 1956b), Jackson and McFadden (1954) and Odum (1957) applied this method to a lake and a stream, and Park, Hood and Odum (1958) to coastal water.

Verduin followed the changes of pH in bottles suspended in the lake. He estimated the corresponding variation in CO_2 in reference to the pH-CO_2 relation curve which was previously constructed from data for pH variation of the same lake waters. Verduin's procedure, however, has been criticized by Beyers and Odum (1959) and Lyman (1961). In spite of these criticisms Verduin has maintained his stand, and to date a dispute continues between them (Beyers and Odum, 1960; Verduin, 1960a, 1960b, and 1961).

It will be appropriate here to touch on the reliability and sensitivity of the pH method of Verduin. In western Lake Erie, a pH change of 0.1 unit represents a CO_2 change of about 12 μ mol/l. In ocean water, however, the Beckman type pH-meter would indicate CO_2 change to be only about one-fifth as sensitive as for lake water. From these considerations, the pH method seems rather to be restricted to fresh water with low buffer capacity.

According to Verduin (1960a and 1960b), the value of photosynthesis obtained by the carbon-14 method is often two times higher than that of the pH method, and the value of the latter is two times higher than that of the usual oxygen-bottle method. It is also observed that the pH changes inside the suspended bottles are nearly one-half of the pH changes in the surrounding water milieu. However, Frey and Stahl (1958) compared the values obtained by the carbon-14 and pH methods in the same samples of two arctic lakes and found fairly good agreement.

2. Oxygen method: The original idea of estimating production from the photosynthetic rate of phytoplankton was first presented by Gaarder and Gran (1927). They deduced photosynthesis from the amount of oxygen produced by phytoplankton during a given time. Water samples collected from various depths were distributed into two sets of glass bottles, transparent and dark. The bottles were then suspended at the particular depth from which each sample was taken. After a given time, 24 hours or more, the oxygen content of the bottles was determined by the Winkler estimation. From the difference between the initial and the final concentration of oxygen, net production was obtained in the transparent bottles and respiration in the dark bottles. However, it should be noted here that the decrease of the oxygen in the dark bottles resulted from the consumption of the oxygen not only through respiration of phytoplankton and other organisms, but also through the decomposition of organic debris in the water. It should also be noted that the condition inside the dark bottle favors the growth of bacteria which re-

sults in the overestimation of the gross production. Nevertheless, the oxygen method has been widely employed in the field of ecological research because of the ease with which it can be used. By the Winkler estimation, we can determine accurately the oxygen content of 0.05 ml/l, and the assimilation of 0.02 mg/l can be detected reasonably. Therefore the oxygen method is quite efficient in eutrophic water. Riley, Stommel and Bumpus (1949) applied the oxygen method to oceanic waters, and Vinberg (1958) and Odum (1957) have further assessed production from the diurnal change in the oxygen content of waters.

3. Carbon-14 method: A more sensitive method of measuring photosynthesis in natural phytoplankton was recently introduced by Steemann-Nielsen (1952). He employed a new technique, the use of radioactive carbon during the "Galathea" expedition (1950-1952) in many of the oceans throughout the world.

General procedure: In this method, after the addition of a definite amount of carbon-14 in the form of a carbonate, the water sample is exposed to light for a given number of hours. After exposure, the water sample is filtered and the amount of carbon-14 fixed in the plankton cells is determined. The amount of the assimilated carbon can be calculated from values such as the total amount of CO_2 in the water samples, and the ratio of radioactivity of the added tracer to that accumulated in phytoplankton. If the salinity, temperature and pH are known, the amount of total CO_2 in the sample water can be calculated from the table proposed by Buch (1951) and others. This CO_2 calculation can be dispensed with for pelagic waters, since it is sufficient to put the value of total CO_2 as 90 mg/l. For the fresh and brackish waters, however, it is desirable to measure total CO_2 directly, because in these waters the calculated total CO_2 deviates sometimes to a degree of 100% or more from that measured directly. Among the methods for the direct measurement of total CO_2 in the water, the following are recommended: Sugawara (1939), Koyama (1953), Saruhashi (1953) and Saijo (1956). The procedure of the carbon-14 method and related techniques such as sampling of water, preparation of the carbon-14 tracer ampoules, incubation, filtration, etc., are precisely described in the following papers: Steemann-Nielsen (1952), Steemann-Nielsen and Aabye Jensen (1957), Sorokin (1956 and 1959), Jitts (1957), Doty and Oguri (1958) and Angot, Doty and Oguri (1958). From the technical angles, Doty (1954-1960) examined each step of the procedure in detail and discussed the results in a series of papers.

Measurement of production by the carbon-14 method: To determine production under field conditions, the carbon-14 method is so far employed in three different ways.

a. The "in situ" method process: This procedure is quite similar to the method of Gaarder and Gran's described above, except for the addition of tracer to the water sample. A half daytime exposure, from sunrise to noon or noon to sunset, is usually recommended, whereby errors resulting from a prolonged enclosure of the sample in the bottle are minimized. This procedure is conveniently applied to lakes and littoral regions of the sea, but is impracticable on the open sea because of the inconvenience of keeping the boat at a specified point for a long time.

b. The "tank" method process: This method was suggested by Steemann-Nielsen (1952) to overcome the disadvantage of the "in situ" method described above, and it has been used by many oceanographers. The bottles, instead of being suspended, are placed in a water tank in the ship's laboratory and are exposed for a given time, usually 4 hours, to artificial light of nearly saturating intensity. During this exposure the water temperature in the tank is kept the same as that of the surface water of the sea. Daily production per unit area is calculated from data, such as photosynthesis rate obtained by the above procedure, the underwater illumination simultaneously observed, and the photosynthesis-light curve. For simplifying this calculation procedure, Steemann-Nielsen (1952) proposed a useful empirical formula.

The principle of the tank method neglects the fact that optimum light intensity is variable with depth, especially when the water is stratified. Consequently, this point must be taken into consideration upon application of this method.

c. The "modified tank" method or "simulated in situ" method: This method originated from Riley's "light and dark bottle method," but in this case bottles are placed in a tank on the deck and are exposed to daylight. However the light is screened by plates of neutral glass so that the intensity falling on the bottles can simulate the actual light intensity at the depth from

which the sample was collected. Among many suggested methods, this procedure may be the most convenient for the practical purpose of measuring organic production in the ocean.

Some problems on carbon-14 measurement: Some physiological factors which affect the interpretation of the carbon-14 method for measurement of production will be discussed later by Thomas, but here are some problems which should be considered here in relation to this subject.

a. Dark fixation of carbon-14: It is well known that dark fixation of carbon is usually 1-3% of photosynthesis at light saturation. However, high values for dark fixation are often obtained in polluted waters as well as in unproductive waters scanty in nutrients. Recently Steemann-Nielsen (1960a) reviewed this problem and emphasized the difference between the dark fixation due to the Wood-Werkmann reaction and the so-called chemosynthesis. At present we have no means by which these two different kinds of processes can be separately determined, although Sorokin (1958b) used the carbon-14 technique for estimating the rate of chemosynthesis in the sea.

Putting aside this problem, there is great need for simultaneous determination of the dark fixation in the determination of photosynthesis by the carbon-14 method. The value of the dark fixation must be subtracted from that of the light bottle to obtain a corrected light value.

b. Daily periodicity of photosynthetic rate: Doty and Oguri (1957) pointed out that in the tropical Pacific there is a daily periodicity in the photosynthetic rate under the saturated light. This phenomenon was confirmed by many researchers, e.g., Shimada (1958) and Yentsch and Ryther (1957). Furthermore, Verduin (1957) and Ohle (1958) found the same periodicity in lakes. Daily periodicity usually shows the maximum rate in the morning and the minimum at midnight. However, a drop in the rate is often observed earlier in the evening. At the surface, the maximum reaches 1.5 times the minimum in temperate waters and 8 times the minimum in tropical waters. Time of day, therefore, is an essential factor for a comparative study of photosynthetic rate, consequently, during cruises, sampling and determination must be carried out at a specified time of the day.

c. Determination of the respiration rate: In a topic concerning the carbon-14 method, it will be appropriate here to add the application of carbon-14 to the determination of the respiration rate of phytoplankton. Steemann-Nielsen and Hansen (1959a) tried to extrapolate the photosynthesis-light curve to determine the respiration, and succeeded for samples of natural waters by showing that the respiration is about 10% or less of the photosynthesis at the light saturation point.

IV. ESTIMATION OF PRODUCTION FROM CHLOROPHYLL AMOUNT

As a measure of standing crop of phytoplankton, chlorophyll and other pigments were first used by Harvey (1934) in the ocean and by Kozminski (1938) in lakes. The spectrophotometric determination of chlorophyll by Richards with Thompson (1952) facilitated the separate determination of chlorophyll-a, -b, -c and carotinoids in oceanic water. Discussion of the techniques and coherent problems will be omitted here because these topics appear to stray from the scope of the present paper. However, the following papers are suggested for reference: Krey (1958a), Odum, McConnel and Abbott (1958), Humphrey (1960) and Strickland (1960).

The estimation of primary production based on chlorophyll and light data was initiated by Manning and Juday (1941) in nine Wisconsin lakes. This method has further been used by Gessner (1944), Hogetsu and Ichimura (1954), Saijo (1956) in lakes, and by Ryther and Yentsch (1957), Menzel and Ryther (1960), Ichimura and Saijo (1959) and Saijo and Ichimura (1960) in the ocean.

In the so-called "chlorophyll method," production calculation is performed in the following manner. From the measurement of the light intensities at various depths, a light-depth curve is constructed in which the light intensities are shown as relative values of the light intensity at the surface of the water. The diurnal change of the light intensity is determined at the surface as an absolute value. Therefore it is possible to calculate the daily change in light intensity and the photosynthesis-light curve. Two types of photosynthesis-light curves are usually employed: one, the actual curve obtained on shipboard at every station and here the

photosynthetic rate is indicated per unit amount of chlorophyll; the other, the general curve which is previously constructed in the laboratory on land. In the former case the amount of chlorophyll at each depth is multiplied by the integrated daily photosynthetic rate to give the daily production at every depth. The total of these differentials is nothing but the total amount of daily production of a column of water with unit area. In the latter case, the general photosynthetic light curve should be reconstructed by putting the assimilation number on the light saturation point of the general curve. Here the assimilation number should be determined. Pertaining to this subject, it is well known that chlorophyll activity varies with differences in the environmental conditions, especially in temperature, light intensity, nutrient salts and, moreover, with the physiological conditions of organisms. Some authors such as Holmes, Schaefer and Shimada (1957), Rodhe, Vollenweider and Nauwek (1958), Ichimura and Aruga (1958), etc., found that the number is fairly constant during a given period in a certain water body, but it can change seasonally and spatially. On the other hand Manning and Juday (1941), Gessner (1960), Edmondson (1955), Ryther and Yentsch (1958), etc., reported that the assimilation number is fairly constant. As the average assimilation number in natural phytoplankton, Manning and Juday (1941) used 6.7 mg O_2/mg Chl/h in the lake, and Ryther and Yentsch (1957) proposed 3.7 mg C/mg Chl/h in the ocean. In this respect, Saijo and Ichimura calculated production in the western Pacific using a mean value of 1.5 mg C/mg Chl/h in the Kuroshio area and 3.7 mg C/mg Chl/h in the Oyashio area.

According to the results obtained by Hogetsu and Ichimura (1954) in Lake Suwa, production values measured simultaneously by the chlorophyll and "in situ" methods coincide fairly well with each other. Ryther and Yentsch (1957) also proved the coincidence of the values obtained by these two methods in coastal waters. Holmes, Schaefer and Shimada (1957), however, failed to prove the coincidence in values measured by the chlorophyll and carbon-14 methods.

In conclusion, it can be said that a rough estimation of production may be possible assuming a constant assimilation number, but for more precise estimation it is desirable to seek proper values applicable at least for several groups of environmental conditions. Naturally, efforts must be continued in the critical examination of the chlorophyll method and extended to compile necessary information as to the relationship between chlorophyll activity and environmental conditions. Besides the assimilation number we must consider the following matters in due time: inactive chlorophyll, diurnal fluctuation of chlorophyll content in the water, ratio of chlorophyll-a, -b, -c and the character of the photosynthesis-light curve.

a. Inactive chlorophyll: Gillbricht (1952) and the other investigators have indicated that the chlorophyll measured in the sample water is often partly inactive. Furthermore, some other pigments such as chlorophyll derivatives are probably determined as chlorophyll. Therefore, if calculation of production is made without consideration of the foregoing fact, the result obtained may become greater than that by the "tank" or "in situ" method. However, recent research of Steele and Baird (1961) proved that the deviation of assimilation number is quite insignificant in the upper euphotic zone where the greater part of production is performed. Such being the case, the effect of the inactive chlorophyll may be insignificant in production which deals with total matter production in a water column. Thus, it may be that the chlorophyll method gives reliable results even though inactive chlorophyll may be concerned.

b. Diurnal fluctuation of chlorophyll content in water: Shimada (1958) and Ryther and Yentsch (1957) found the daily periodicity in photosynthetic rate paralleled the periodicity of chlorophyll content in the water. However, this periodic change in chlorophyll content is limited to the uppermost layers. That total production in a vertical column of water is little affected by this variation of chlorophyll content was actually proved by Ichimura (1960a) in his observation of some Japanese lakes. On the contrary, when productivity is deduced only from the chlorophyll measured in the surface water, the results are affected by the diurnal fluctuation of chlorophyll content. In natural marine phytoplankton, Yentsch and Scagel (1958) observed that the highest cellular concentration of chlorophyll and carotinoid pigments corresponded to the optimal light intensity for photosynthesis. Therefore, it is very necessary that the sampling and filtration of chlorophyll be made at a certain time of the day.

c. Ratio of Chlorophyll-a, -b, -c: The physiological effect of chlorophyll-b and -c on photosynthesis is comparable to that of chlorophyll-a, but the so-called assimilation number usually refers to chlorophyll-a in the field of marine ecology. Now the future problem is to clear the

quantitative magnitude of each chlorophyll component and to elucidate what could be the roles of chlorophyll-b and -c.

d. Light adaptation of phytoplankton and temperature effect on photosynthesis: Under stratified conditions, the phytoplankton in the deeper layer has its maximum photosynthetic rate at lower light intensities than the plankton growing near the surface. This so-called "light adaptation" phenomenon of phytoplankton has been observed by Steemann-Nielsen and Hansen (1959b), Rodhe, Vollenweider and Nauwek (1957), Ryther and Menzel (1959), Talling (1960), etc. Light adaptation also appears seasonally and spatially. For this reason, it is desirable to modify the form of the general photosynthesis-light curve used in each case in the calculation of production. Because of this, the form of the curve should be examined in the samples taken from several stations.

Special care must also be taken in regard to temperature when samples collected from deeper layers with lower temperature are subjected to the carbon-14 test in a tank with a temperature higher than that of the deeper layer.

ISOTOPIC AND OTHER TECHNIQUES FOR MEASURING BENTHIC PRIMARY PRODUCTION*

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INTRODUCTION

Benthic populations can be known to be significant producers only when their production has been estimated on an area basis, and preferably when all primary producers in a region have been considered and ranked in relative importance. This has been done in relatively few places. With few exceptions, our knowledge of the production of benthic plants consists of measurements of the production of some particular population, usually one that is dominant or at least obvious. Enough measurements of this sort have been accumulated to suggest that in some shallow-water environments benthic plant populations make major contributions to the primary productivity of an embayment or coastal region. A number of such observations have been brought together in Table 1. Evidently it is not unusual for production of benthic plants to exceed that of phytoplankton per unit area in shallow waters. Undoubtedly some benthic populations are more efficient than are phytoplankton in utilizing the available light. Attachment to the bottom makes a population less susceptible to removal by water currents and probably enhances the exchange of dissolved materials.

Among the most obviously productive coastal areas are the coral reefs, although they are often in regions where planktonic productivity and the standing crop of plankton are small. Yonge and associates (1931-1940) pointed out the possible importance of symbiotic algae in the food relations of reef organisms. Sargent and Austin (1949 and 1954), Odum and Odum (1955), and Kohn and Helfrich (1957) have shown coral reefs are self-supporting systems. That is, primary production on the reef is at least meeting the requirements of the higher trophic levels of the system. They have provided good evidence that symbiotic algae in the reef corals are important producers, as well as *Porolithon* and the more obvious large, attached algae. Odum and Odum pointed out the presence of blue-green algae in the skeletons of reef corals and presented some evidence that they may be as important as the well-known zooxanthellae as producers. Doty (1958b) emphasized the importance of *Porolithon* as a builder of the windward reef front of many atolls and the probable importance of blue-green algae as stabilizers of loose sediments and as fixers of nitrogen.

The relative importance of the various plant populations in primary production on coral reefs is not known. Measurements of oxygen production of enclosed corals suggest that their symbiotic algae are important. A single observation with enclosed *Porolithon* (Sargent and Austin, 1954) suggests that it may be as important a producer, per unit area, as the symbiotic

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Table I. — Productivity of Benthic Marine Plants

Population	Location	Production in terms reported	g. C/m^2/day†	Source	Method
Laminaria	Scotland and California	66 g. dry matter/m^2/day	9.	Blinks, 1955	O_2 bottles
Pelvetia	California	35 g. dry matter/m^2/day	5.	Blinks, 1955	O_2 bottles
Fucus	California	19-42 g. dry matter/m^2/day	2.-5.	Blinks, 1955	O_2 bottles
Alaria	California	14 g. dry matter/m^2/day	2.	Blinks, 1955	O_2 bottles
Egregia	California	25 g. dry matter/m^2/day	3.	Blinks, 1955	O_2 bottles
Iridophycus	California	19 g. dry matter/m^2/day	2.	Blinks, 1955	O_2 bottles
Gigartina	California	54 g. dry matter/m^2/day	7.	Blinks, 1955	O_2 bottles
Porphyra	California	11-21 g. dry matter/m^2/day	1.-3.	Blinks, 1955	O_2 bottles
Ulva	California	3-7 g. dry matter/m^2/day	0.4-1.0	Blinks, 1955	O_2 bottles
Zostera marina	Denmark	277 g. dry matter/m^2/year	0.3?	Grøntved, 1958	harvest
Ruppia maritima	Denmark	140 g. dry matter/m^2/year	0.2?	Grøntved, 1958	harvest
Chara spp.	Denmark	283 g. dry matter/m^2/year	0.3?	Grøntved, 1958	harvest
Zostera marina	Denmark	500-2000 g. dry matter/m^2/year	0.6-2.5?	Petersen, 1913	harvest
Zostera + *Ruppia*	Denmark	184 g. dry matter/m^2/summer	0.2?	Grøntved, 1960a	harvest
Microbenthos	Denmark	0.11-0.22 g. C.*	0.6-1.1	Grøntved, 1960b	C^{14} bottles
Microbenthos	Georgia, U. S. A.	0.4-1.0 g. C/m^2/day	0.4-1.0	Pomeroy, 1959	O_2 bell jars + CO_2 gas
Symbionts in *Pocillopora*	Rongelap Atoll	.042 ml. O_2/g. dry wt./hour		Sargent & Austin, 1954	O_2 bottles
Symbionts in *Acropora*	Rongelap Atoll	.035-.075 ml. O_2/g. dry wt./hour		Sargent & Austin, 1954	O_2 bottles
Porolithon	Rongelap Atoll	.046 ml. O_2/g. dry wt./hour		Sargent & Austin, 1954	O_2 bottles
Coral reef community	Rongelap Atoll	12 g. glucose/m^2/day‡	4.‡	Sargent & Austin, 1949	diurnal O_2 curve
Coral reef community	Eniwetok Atoll	24 g. glucose/m^2/day‡	7.‡	Odum and Odum, 1955	diurnal O_2 curve
Coral reef community	Hawaii	7.7-8.3 g. C.m^2/day‡	7.7-8.3‡	Kohn & Helfrich, 1957	diurnal O_2 curve
Thalassia testudinum	Long Key, Florida, U. S. A.	34 g. O_2/m^2/day‡	10.‡	Odum, 1957	diurnal O_2 curve
T. test. + microbenthos	Boca Ciega Bay, Fla. U. S. A.	5‡ g. O_2/m^2/day	2.‡	Pomeroy, 1960a	diurnal O_2 curve
Macrocystis pyrifera	California	15 g. dry matter/m^2/day	2.	(Sargent) Emery, 1960	diurnal O_2 curve
Spartina alterniflora	Georgia, U. S. A.	4248 K Cal/m^2/year	5.	Smalley, 1959	harvest

*Expressed as "potential productivity." To estimate daily production in g.C/m^2/day, use the factor, hours of daylight/2.

†To make the findings more readily comparable all have been converted to grams of carbon per square meter per day. The conversions are necessarily approximate in some cases.

‡Gross production. All other values are net production.

algae. The blue-green algae that are abundant in both living and dead corals and in submerged reef rock and shingle deserve further attention.

The lagoons of atolls usually are populated with plants even at their maximum depths (Doty, 1958b; Gilmartin, 1960). Probably lagoons are much less productive than reefs, per unit area, but since their area is often one hundred times that of the reefs they may contribute significantly to the overall productivity of atolls. Many such details remain to be investigated.

The primary productivity of fjords has been the subject of several investigations over a period of nearly fifty years (Petersen, 1912 and 1915; Boysen-Jensen, 1941; Printz, 1950; Grøntved, 1958, 1960a and b). These studies have included both the phytoplankton and the benthic plants. Estimates of the production of kelp and other economically-important seaweeds have been made widely, including those reported by Tkihovskaya (1940), Alleem (1956), Sargent and Lantrip (1952), and Walker and Richardson (1955). Not all of these have been useful in estimating primary production for reasons that will be given in the section on harvesting methods.

The productivity of shallow embayments has been estimated in Puerto Rico (Odum et al., 1959), Florida (Odum, 1957; Pomeroy, 1960a), Texas (Odum and Hoskins, 1958), and Georgia (Smalley, 1959; Pomeroy, 1959; Teal, 1959). Most of these studies showed that benthic populations are more productive than phytoplankton in many shallow embayments. The productivity of intertidal populations has been estimated by Grøntved and the Georgia group. These populations include both the microscopic diatom populations in the sediments and such macroscopic plants as Spartina alterniflora. Golley et al. (in press) give evidence that mangroves are not important producers, at least in the location in Puerto Rico where their production was estimated. The marine grasses may be highly productive under optimal conditions (Odum, 1957; Odum et al., 1959) or moderately productive near the edge of their geographic range (Pomeroy, 1960a).

Present and Potential Methods

Methods for estimating the production of benthic plants have been derived largely from modifications of methods used in other terrestrial and aquatic situations. Many of the methods for measuring the production of phytoplankton have been modified for benthic work. The recent reviews of techniques for measuring the production of phytoplankton contain much that is useful to those working with benthic populations (Lund and Talling, 1957; Strickland, 1960; Talling, 1961). No single method has been found to be best in all situations, and in a given case the investigator must decide which method is most suitable for his intended purpose, modify it as needed, and then critically evaluate its accuracy as it is actually used by him.

A. Harvesting the standing crop.

It might seem that harvesting at well-chosen times is the best and easiest method of estimating the production of plants, especially large ones. Often it is neither. Harvesting is justified when the information wanted is the amount of organic matter that can be harvested. When an estimate of total primary production of organic matter is wanted, harvest methods do not give a direct answer, and it is difficult to get an answer by such methods without an elaborate experimental program. The amount of organic matter that can be harvested from a plant population is the amount that has not been eaten or worn away during the period of growth. The amount that is lost in these ways will vary with the species and with the environment. Blinks (1955) presents a comparison of standing crop with production as estimated from the rate of evolution of oxygen by the plants. The time required to generate the crop varied from ten to one hundred days, with no correlation with the size of the standing crop. A non-critical estimate of production from standing crop data might be wrong in order of magnitude.

When harvests do yield the kind of information wanted, they can be done with predictable precision (cf. Walker and Richardson, 1955). Sometimes, however, they seem to be used without full appreciation of their shortcomings or of the alternatives that are available.

B. Chlorophyll and incident radiant energy.

Ryther and Yentsch (1957) have developed a method for estimating the production of phyto-

plankton in the sea from information on the amount of chlorophyll-a found, the amount of light at the sea surface, and the transparency of the water. This method can be applied to benthic plant populations only after a critical consideration of some differences between the benthic and planktonic situations. Sediments frequently retain relatively large amounts of pheophytin-a and pheophorbide-a. Their spectrophotometric separation from the chlorophyll-a in living cells presents a difficult problem (Orr et al., 1958). The assimilation number varies rather widely among various plant populations, and the mean value used for phytoplankton cannot be applied to other plant populations. Enough estimates of the assimilation number of various plants have been made to suggest its range, and this is not encouraging (Odum et al., 1958). Values from 0.5 to 80 g./g./hour have been reported. Probably we do not know enough about the assimilation number of any benthic plant population to permit an estimate of production that will be within one order of magnitude of the true value. Important discussions of the problems of light-and-pigment methods are in the papers of Odum et al., (1958) and Strickland (1960).

C. Evolution of oxygen.

The well-known light-and-dark-bottle method has been modified in several ways for use with benthic populations. One modification is the use of bell jars placed directly over the plants on the bottom. Filtered water may be placed in the bell jars to eliminate phytoplankton photosynthesis, although often this proves to be trivial. On hard bottoms a band of flexible rubber may be put around the bottom of the jar as a seal (Odum and Odum, 1955). Usually the changes in oxygen in the bell jars are estimated by the Winkler method, but it is possible to obtain a continuous record of changes in oxygen tension by using platinum-silver oxide polarographic electrodes with a suitable recording potentiometer (Carritt and Kanwisher, 1959; Kanwisher, 1959). Mr. R. B. Williams is currently using this method to study intertidal sediments at the University of Georgia Marine Institute. The silver-lead galvanic cell of Hersch (1960) might also be adapted to field use.

When working with the larger marine algae and marine spermatophytes it may be more convenient to place known amounts of the plants in bottles, particularly where the bottom is not readily accessible. Production can then be estimated from standing crop data. With sufficient replication this approach should offer a great improvement over the usual standing-crop methods. Some precautions must be taken that are not necessary in most work with phytoplankton. Not only must light be duplicated faithfully, but so must the supply of carbon dioxide. Large masses of plants must not be placed in small bottles. The duration of the experiment may be as little as one hour. A check on the initial and final pH of the water in the bottle will give assurance that CO_2 has not been depleted during the experiment.

The inherent limitations on the accuracy of methods based on oxygen evolution are discussed by Strickland (1960). These methods can provide useful data with a minimum of equipment and supplies, if reasonable care is taken in working out the details of procedure according to circumstances.

D. Uptake of carbon dioxide.

The uptake of carbon dioxide can be measured either from changes in the pH of the water (in bottles, bell jars, or open water) or by the addition of $HC^{14}O_3$ to the water (in bottles). The latter method (Steemann-Nielsen, 1952) is very sensitive and potentially very accurate. Recently the method has been modified for estimating the production of benthic microflora by Grøntved (1960b). He collects a core sample of the sediments, suspends an aliquot in filtered water, and adds $HC^{14}O_3$. The suspension is held in the sun, with periodic shaking, for two hours, after which an aliquot is filtered and the carbon-14 on the filter is counted. From this Grøntved gets what he terms "potential production". He suggests that real production is half the "potential production". The method in its present form does not seem to be more accurate than others, although it is undoubtedly sensitive to small changes. However, it probably represents the first successful use of a radioisotope for routine estimates of production in nature and essentially in situ. We can expect to see further modifications of it to suit other conditions.

E. Uptake of nutrient and trace elements.

Estimates of photosynthesis based on measurements of the rate of uptake of carbon dioxide or $HC^{14}O_3$ are directly and immediately related to the photosynthetic process. It is also possible to correlate production with other basic processes, such as the formation of new protoplasm or the uptake of any of several constituents of protoplasm. Both phosphorus and nitrogen are present in protoplasm in quite constant proportions, and their rates of uptake should be proportional to the rate of production of protoplasm (i.e., net production). No method based on the uptake of nitrogen has been developed as yet. The existence of several different forms of available nitrogen and the preferential uptake of different ones by different plant species or higher taxa present a problem. However, it may be possible to label with nitrogen-15 when more is known about the turnover times of the inorganic forms of nitrogen in natural waters. Some work along these lines has been done (Dugdale *et al.*, 1959).

Phosphorus is a more likely choice as an indicator of photosynthesis, and the chemical measurements of long-term changes in dissolved phosphate in the sea have been used with some success to estimate the production of phytoplankton (Riley, 1951 and 1956; Steele, 1956 and 1957). In the sea, exchanges with the bottom and the very short-term cycles of phosphorus can be ignored successfully. In shallow waters, exchanges with the bottom must be considered in the calculation (Riley, 1956).

Attempts to use phosphorus-32 in a way analogous to the present use of carbon-14 for short-term estimates of organic production have not been successful. For several reasons, the short-term uptake of phosphorus may not be related to organic production, although in the long run phosphorus is taken up in amounts proportional to net production. The rate of uptake of phosphorus may be proportional to surface area, at least in some circumstances, as suggested by Odum *et al.*, (1958), but unless photosynthesis is limited by the surface area of the plant, uptake of $P^{32}O_4$ will not provide an estimate of production. The calculations of Munk and Riley (1952) suggest that nutrient absorption may limit the growth rate of large plants in still water (for example, in bottles in the laboratory). However, if plants have stored reserves of phosphorus, this may not effect short-term experiments.

The fact that phosphorus is involved in several biochemical processes further complicates attempts to relate $P^{32}O_4$ uptake to photosynthesis. Grube (1953) found an increase of phosphorus-32 in the TCA-soluble fraction of *Elodea* under illumination but he was unable to relate the uptake of either total phosphorus or any fraction that could be extracted to photosynthesis.

Other events that complicate the interpretation of the uptake of phosphorus-32 include sorptive exchanges of phosphate, active biological exchanges of phosphate, and the rapid regeneration of phosphate by bacteria and animals. The turnover time of phosphate in the tropical oceans may be on the order of one to ten hours (Pomeroy, 1960b). The total flux of phosphate would seem to be one or two orders of magnitude greater than the rate of incorporation of phosphorus into new protoplasm by autotrophic organisms.

The indications of very rapid turnover of phosphate in the sea and the failure to relate phosphate turnover to photosynthesis experimentally (Gest and Kamen, 1948; Grube, 1953) suggest that it will be difficult if not impossible to relate the uptake of phosphorus-32 to primary production of either phytoplankton or benthos. A more detailed knowledge of the very rapid cycles of phosphorus in natural waters will be necessary before a method can be developed.

Some of the trace elements that are essential for plant growth may offer possibilities for the development of isotopic methods of measuring production. Zinc is taken up by marine plants in the light and is taken up more slowly or not at all in the dark (Boroughs *et al.*, 1957; Chipman *et al.*, 1958; Taylor, 1960). Bachmann and Odum (1960) suggested that zinc uptake might prove to be a useful parameter of production. However, Gutknecht (1961) found that there is a sorption reaction that is large relative to the active-uptake process. The biochemical roles of zinc are difficult to distinguish from those of magnesium, manganese, and cobalt (Lehninger, 1950), and zinc is taken up by animals as readily as by plants (Boroughs *et al.*, 1957; Chipman *et al.*, 1958). These are some of the difficulties that must be overcome in devising a means of using zinc as a parameter of primary production.

Other trace elements have received less attention from this point of view. Molybdenum is

accumulated by phytoplankton, and the uptake of molybdenum-99 may be more rapid in the light than in the dark in some circumstances (Barsdate and Guillard, 1961). Other trace elements that seem promising on the basis of their known biochemical roles have not been investigated as possible parameters of production.

In exploring the possible application of radioisotopes to the measurement of primary production it is necessary to distinguish between active uptake and exchange. The findings with zinc show the importance of this distinction. The apparent finding of differences in the rate of sorption in the light and in the dark presents an especially dangerous pitfall.

F. Gas analysis for intertidal populations.

In many estuaries there are populations of plants in the intertidal zone that are important producers. These plants are carrying on photosynthesis whenever they are illuminated, whether submerged or not. Methods that are used with terrestrial plants have been modified to estimate production of plants during periods of emergence at low tide. These are methods in which air is passed continuously through a chamber containing the plants, and changes in the gases after passage through the chamber are measured. Carbon dioxide may be collected in absorption columns (Verduin and Loomis, 1944; Pomeroy, 1959; Pochinok, 1957, or it can be measured with an infra-red gas analyser (Golley et al., in press). Both methods are cumbersome in the field, and the accuracy of either will depend largely on the associated instrumentation and the care taken by the operator. A method using gaseous $C^{14}O_2$ might require less bulky equipment and should give high accuracy and sensitivity, but to this writer's knowledge it has not been tried with intertidal marine plants.

G. Evaluation of the production measurements.

In planning production measurements in the field and in evaluating them it is well to remember that benthic plant populations, like phytoplankton, are frequently clumped in their distribution. For this reason, randomized positioning of sampling or in situ measurements is important. The data should be tested for fit with various distributions, and appropriate statistical parameters used. Distributions in time rather than space are more likely to be normally distributed, and the distribution of errors of measurement in replications at one location may be normal. While these precautions are familiar ones, they have not always been observed.

Concluding remarks

Many of the limitations and shortcomings of the methods that have been discussed are the same as those of the related methods for measuring planktonic primary production. Some of these represent very serious problems, but since they are discussed by other contributors to this symposium, emphasis here has been on the special problems of dealing with the benthos. This review has included a large proportion of speculation and discussion about possibilities for new methods, because very little has yet been done with benthic populations and what has been done has been with adaptations of methods intended for phytoplankton or terrestrial plants. These adaptations leave much to be desired. As more investigators become interested in benthic primary production, new and better methods of measuring it should be developed. Radioisotopes offer several advantages, and they are not yet fully utilized in this work. While carbon-14 seems to be the most promising isotope at this time, other possibilities do exist that merit further investigation.

THE MEASUREMENT OF PRIMARY PRODUCTIVITY AND LIMITING FACTORS IN FRESHWATER WITH CARBON-14

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1. INTRODUCTION

Interest in primary productivity has had considerable impact on quantitative biology in recent years. To find the origin of this interest one must go back to the early diagrammatic food webs of Shelford (1913), Naumann (1925), Perfiliev (1929) and MacFadyen (1948). In setting down these illustrations, oversimplified as they necessarily were in view of limited knowledge, a greater insight was gained as to the probable relationship of the various food levels. This conceptual development probably gained much from the earlier recognition by Forbes (1887) that the organisms within a lake are interdependent, with a high mutual sensitivity to changes within their organic complex.

With the development of limnology, the organismal community approach to aquatic biology gave ground to viewing lakes as ecosystems. Lindeman (1942), proposing the trophic-dynamic view of ecology, believed that to apply the community approach to lakes was to force a biological emphasis on a more fundamental system. The importance of his contribution lay less in the semantics of the problem than in recognition of the importance of rate measures, and in the interest generated in better quantifying the rate functions.

Interest in energy transformation with the application of the laws of thermodynamics helped to establish that rates were more meaningful measurements than standing crop. The problems arising from confusion of biomass and energy are discussed by MacFadyen (ibid.).

The rate of carbon fixation at the level of the primary producers currently provides the best assessment of the result of the interactions of the host of physical, chemical, and biological factors which determine the actual fertility of any environment. The methods of measuring primary productivity have been frequently reviewed (Steemann-Nielsen, 1952, 1960b; Ryther 1956b; Lund and Talling, 1957; Strickland, 1960), and their development has served to focus attention on the autotrophic organisms which are the first to utilize energy in the food cycle. Certainly the photosynthetic forms are more important, with chemosynthetic ones taking a minor position in the productivity of most environments (Kuznetsov, 1956; Steemann-Nielsen, 1960a). In a dichothermic lake, however, Jackson and Dence (1958) suggest that the purple sulfur bacteria are the most important primary producers and serve as the major food source for the zooplankton.

The development of the carbon-14 technique was a recognized advancement in sensitivity, and has been essentially unchanged since its introduction by Steemann-Nielsen (1951a, 1952). The use of carbon-14 in freshwaters has steadily increased in recent years. The earliest published work appears to be that of Kuznetsov (1955), Nygaard (1955), Sorokin (1955, 1956), and Rodhe (1957). An attempt has been made to examine these and the more recent freshwater work utilizing carbon-14. Each investigator according to his individual inventiveness tends to adapt the carbon-14 method to the environment in which he works and to the facilities at his disposal. It seems desirable at this time to consider these variations and to suggest a some-

what standardized procedure for freshwater work. Certainly, uniformity of technique would aid in improving the comparability of data from different lakes of the world.

2. THE MEASUREMENT OF PRIMARY PRODUCTIVITY

a. Laboratory methods

(1) Absolute activity in gas phase. A good deal of the sensitivity of the carbon-14 technique can be lost in assay of the sodium carbonate solutions and in determining the activity of collected samples. Both practical and theoretical considerations of available evidence on back scattering and self absorption of standards and of filtered algae indicate that the use of absolute activities with the same geometry as that of the test materials is desirable in calibration. Determination of the absolute activity of sodium carbonate solutions and of counting machine efficiencies, in freshwater studies as in marine, traditionally have been based on $BaC^{14}O_3$ standards extrapolated to zero thickness. Vinberg and Kaler (1960) report that because of self scattering of the beta emission, extrapolation to zero thickness with inadequate points on the initial curve has led to overestimates of carbon uptake of from 20 to 25%. Jitts (1957) has attempted to circumvent this problem by assuming self-absorption to be exponential. Because this assumption is not strictly valid, Jitts and Scott (1961) and Jitts (1962) have used a thin film of labeled plastic whose absolute activity was determined by liquid scintillation counting.

In using either a barium carbonate or a plastic film standard for determining the efficiency of a machine, one makes the tacit assumption that any back-scattering or self-absorption encountered in the filtered plankton will be of the same magnitude as that of the standard. The necessity of making these assumptions can be eliminated by making calibrations in gas phase (Goldman, 1960a). A similar but more time consuming method for standardization of carbon-14 measurements with a Lauritsen electroscope in gas phase is described by Miyake et al. (1954).

Because of the low energy beta emission of the carbon-14 atom (0.155 Mev), the presence of diatom populations, and suspended volcanic ash in some of the Alaskan lakes studied by the author, it seemed unwise to assume that the geometry of filtered barium carbonate was identical with the geometry in measuring the activity of filtered algae. To circumvent this difficulty, calibration of the Gieger-Mueller (G. M.) counting equipment was made from labeled algae whose absolute activity was then determined in gas phase according to the method of Bernstein and Ballentine (1950), after a wet combustion to CO_2 (van Slyke and Folch, 1940). The absolute efficiency of the gas phase unit was determined by combusting a National Bureau of Standards sample. By removing the carbon-14 from the algae or sodium carbonate solutions and counting it as $C^{14}O_2$, the problems of self-absorption and back-scattering were eliminated, and one could deal entirely in terms of absolute activity. The calibration of the counting equipment had an accuracy of ±2%.

The availability of extremely sensitive electrometers with wide activity range (e.g. Nuclear Chicago Dynacon Model 6000, or Cary Model 31, vibrating reed electrometer), complete with ion chambers, converter assemblies, and glassware systems for carbon dioxide generation, has greatly facilitated the use of gas phase for routine analysis and in calibration of G. M. counters.

(2) Preparation of carbon-14. Steemann-Nielsen's method (1952) for the preparation of $Na_2C^{14}O_3$ is equally applicable to freshwater studies. It is strongly advised that the final solutions be prepared in one large lot in the activity range of 2-5 microcuries per ml to eliminate variability in activity during the course of a study. To increase the efficiency of CO_2 absorption by the NaOH solution, a glass covered magnetic stirring bar can be used in the NaOH solution of the combustion flask. This may prevent the NaOH from developing a pH gradient which will reduce the efficiency of the conversion.

The use of KOH instead of NaOH (Sorokin, 1959) is not recommended, since K^+ is frequently in low supply and may actually be a limiting factor in some environments (Goldman, 1960b). The water used in dilution should be de-ionized and glass-distilled as a further safeguard against trace element contamination. In the waters assayed, the HCl used in adjusting

the pH of carbon-14 solutions does not appear to have a deleterious effect on photosynthesis. If the carbon level is so low in the water assayed that it may become limiting during the incubation, use of added carrier carbon as carbonic acid to adjust the pH of the solution is suggested. Although the addition of a milliliter of pH 9.5 NaOH solution (3.16×10^{-5}M) to 125 ml of lake water will not alter the pH significantly, where waters of low pH and buffering capacity are encountered, it may be desirable to adjust the pH of the solution below 9.5. In this case special care must be taken to prevent CO_2 exchange during storage and use.

(3) G. M. Counting. There appears to be general agreement that ultra-thin window gas flow G. M. detectors give more consistent results than windowless types. The loss in efficiency from a thin window requires more counting time but, if used with an automatic sample changer, it is not a serious consideration. Doty and Oguri (1958) have illustrated the use of a standard sample for correcting the efficiency of their machine to a standard value. It is wise to use as unity an average count rate of the standard sample made at the time the efficiency of the machine is determined. If the standard sample is not damaged the efficiency of the machine for counting algae need only be checked once, as changes in efficiency by variation in counting gas, detector windows, or plateau can be corrected for by re-counting the standard.

Because sample disintegrations follow a normal or a Poisson distribution, the square root of the total counts closely approximates the standard deviation. Where automatic counting is used, a total count of 4,000 or 5,000 provides greater accuracy than the other sources of experimental error. If manual counting is used a reduction to 2,000 may be necessary, but should be avoided if possible.

(4) Filtration of samples. Filtration of samples is a variable in methodology worthy of consideration. A variety of pore sizes, filter diameters, and vacuums have been applied to samples by various workers. In twenty freshwater papers reviewed, the membrane filter with porosity of 0.5μ as used by Steemann-Nielsen (1952) was the most widely employed. Jonasson and Mathiesen (1959) used a 0.4-0.8μ and Fogg (1958) used a 0.5-1.0μ. The HA Millipore (0.45 ± 0.02 μ) was used by Frey and Stahl (1958) and Goldman (1960a). Lasker and Holmes (1957) have concluded that it is advisable to employ filters with a porosity no larger than 0.45 μ, after testing 0.3, 0.45 and 0.8 μ filters. As important as standardizing to an HA or 0.5 μ membrane filter is standardizing the vacuum used in filtration. The more fragile varieties of algal cells may rupture under high vacuum and lose fixed carbon through the filter (Guillard and Wangersky 1958). Goldman (1960a) did not exceed 15-20 in. of mercury, and has since been using 15 in. of Hg. Diameter of filters would appear less important. On one occasion the author filtered 18 duplicate 50 ml samples on a 25 mm diameter Millipore unit and on a custom filtration unit of 30 mm. The latter size allows faster filtration with greater dispersion of cells and the filters conveniently fit aluminum planchets for counting. A comparison between these duplicate primary productivity samples filtered on the 25 mm and 30 mm units showed no significant difference. With higher plankton concentrations or where larger volumes are filtered, self-absorption might prove significant with the smaller filtering area. For filtering the contents of a 125 ml bottle a standard 47 mm Millipore filtering unit works well. Automatic counting equipment is now available to take these larger filters. Because bottle volumes vary slightly, the filtration of the entire contents will tend to compensate for isotope-to-volume variations.

Exposing filtered samples to fuming HCl has been recommended by Steemann-Nielsen (1952), and should be continued in high pH waters where there is clear evidence of precipitation of carbonate. Fuming HCl treatment appears to give the least variable results with coccolithophores, but errors in decontamination procedure were found to be too high to merit their use (McAllister, 1961). Usually, in freshwaters an acid treatment makes no significant difference and can be omitted, as noted by Rodhe et al. (1958). Under certain circumstances the carbon-14 may be too tightly occluded within inorganic complexes to be removed even by washing with fairly strong acid (Goldman and Mason, in press). Coating filtering units with a silicone preparation such as Desicote (Beckman Instruments, Inc.) is useful in preventing adherence of cells to the glassware. A neutral formalin rinse will serve to arrest biological activity, but distilled water will serve as well to remove any cells from the filtering funnel; and immediate desiccation will adequately preserve the samples. Because a certain amount of carbon-14 may be adsorbed to the cell walls or to particulate matter, rinse volumes should be

the same for all samples. Storage of samples is discussed by Doty and Oguri (1958).

(5) Determination of total carbon. Considerable error in primary productivity studies can be introduced in the measurement of total CO_2 content of the water. More than half of the twenty authors surveyed have used pH and total alkalinity determinations as the basis for their estimates. It is obvious that some standard value, such as the 90 mg CO_2 suggested for pelagic marine waters (Steemann-Nielsen, 1952; Doty and Oguri, 1958; Saijo and Ichimura, 1962), cannot be used in freshwaters as the total carbon values vary many fold. The variable buffering capacity of natural waters as well as the high solubility and rapid diffusion rate of carbon dioxide make determinations involving the measurement of pH somewhat uncertain. More exact gasometric, gravimetric, and titrimetric methods are available and a number have been scrutinized for their accuracy and practicality. Milburn and Beadle (1960) list eleven different methods for comparison with their very accurate conductivity method. In general the better methods involve removal of the carbon dioxide from the samples by acidification followed by manometric measurement (van Slyke and Neill, 1924) or re-absorption of CO_2 in standard alkali. Titrating CO_2 after distillation in alkali is more precise than direct titration (Sorokin, 1959).

The excellent micro-diffusion technique of Conway (1950), although designed for high CO_2 concentrations in small volumes, can be adapted for larger samples (Saruhashi 1953). Gravimetric analysis in a variety of biological materials is discussed by Tinsley et al. (1951). To better evaluate direct titrations in California freshwaters, a conversion train was assembled for connection to a Nesbitt absorption bulb (Fig. 1). In waters of low carbon content two sample jars were used instead of the single unit pictured. This made it possible to use 800 ml of sample. Gravimetric recovery was 99.9 ± 1.7% from the conversion of seven standards made from analytical grade sodium carbonate.

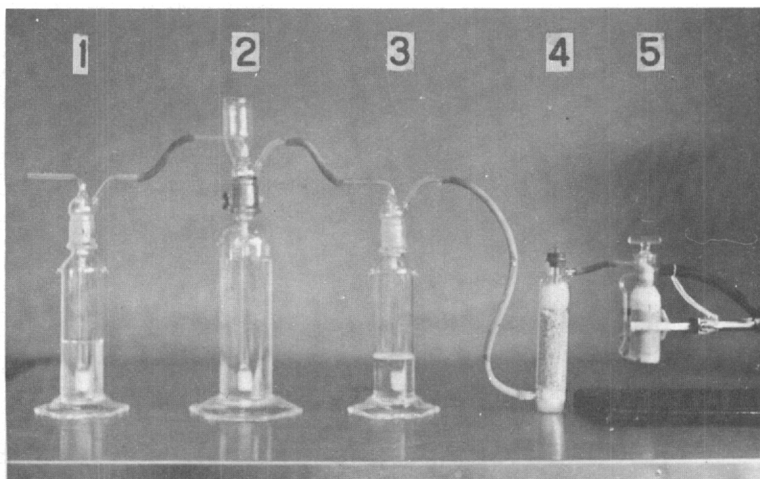

Figure 1—Gravimetric carbon dioxide train. 1: 2N NaOH; 2: water sample, with side vessel of orthophosphoric acid; 3: concentrated H_2SO_4; 4: Orierite tower; 5: Nesbitt tower, connecting to vacuum source.

Using the gravimetric method as a standard, comparisons were made with two other methods of determining total carbon dioxide in lake waters of the area. These were the determination from total alkalinity and pH by use of the dissociation constants of Hutchinson (1957), and the $Ca(OH)_2$ precipitation-EDTA titration method of Berbenni (1960). With only one exception the yields from pH and total alkalinity determinations were lower than the gravimetric by from 10 to 26% (Table I). The EDTA titrations of samples of Lake Berryessa water were within 2% of the gravimetric measurements. Unfortunately this agreement was not repeated with pond water, as recovery from EDTA titrations gave results which were approximately a third too high. The higher organic content of the pond water with much foam formation may have influenced these results. Because of the great variability of natural waters the choice of a carbon dioxide method would appear to merit rather careful attention. There is still a pressing need for a more accurate field method.

Table 1 — A Comparison of Some Gravimetric, pH and Total Alkalinity, and EDTA Titrations for Determining the Total Carbon Dioxide in Fresh Waters. Results Are Expressed in Mg CO_2 Per Liter

Source	Gravimetric	pH-Alk	EDTA titration
Lake Tahoe	44.7	41.4	----
Lake Berryessa	179.3	132.0	176.4
Lake Berryessa	176.0	140.8	173.8
Lab-side Pond	182.7	----	271.9
Lab-side Pond	179.4	----	283.4

b. Field Methods

(1) Lake sampling. *In situ* measurements are desirable when possible, and there is evidence that they still provide the most direct estimation of primary productivity (Talling, 1960a). If comparisons of lakes on the basis of productivity are to have any significance the values presented must obviously be good average values for the lakes in question. Variability of productivity within lakes is well documented (Sorokin, 1959; Goldman, 1960a and 1961a). The former author found that the productivity within Rybinskii Reservoir varied tenfold, and the latter found a consistent increase in productivity towards the inflow end of Brooks Lake, Alaska, as well as lateral differences in relation to inflow springs in Castle Lake, California. It would appear from a comparison of the lakes studied that greater variability in primary productivity within a given lake is associated with greater eutrophication.

In large lakes or reservoirs, regular *in situ* measurements may be impossible; or they may be inadequate to cope with the variation within the lake. Rodhe *et al.* (1958) have compared *in situ* and *in vitro* measurements of primary productivity in Lake Erken and have concluded that the relationship cannot be expressed by a simple factor. Sorokin (1958a and 1959) and Bachmann *et al.*, (1961) have tested a method for shipboard incubation in daylight based on occasional *in situ* measurements. In this manner, Sorokin was able to sample 15 stations while the boat covered over 100 km. Because of the very shallow euphotic zone (3-6 m) only four or five depths were sampled. With the use of a fast boat, Goldman (1960a) was able to collect thirty samples to a maximum depth of 65 m at three stations over a distance of 8 kilometers on Brooks Lake. By collecting all the samples first in an insulated box it was possible to place them all back in the water during the 20 minute return run. Another method of sampling is to provide an index station in some central or convenient location which is sampled at frequent intervals and occasionally simultaneously with more distant stations in the lake. In this manner one can compare both ends of a large lake, using the index station as a point of reference for day to day variation in weather and, in some cases, plankton population dynamics. Amphibious aircraft can also provide a rapid means of covering one or more lakes in a single day, as the author has used conventional limnological gear from the hatch or pontoon of a floating plane. Hand or battery operated vacuum pumps can provide in-flight filtration.

Some generalizations concerning the frequency of measurements certainly are in order. Rodhe *et al.* (1958) show the inadequacy of weekly measurements as representative of temporal variations in productivity in Lake Erken. In northern latitudes one frequently encounters extreme variability in weather conditions from day to day. Goldman (1960a) found that photosynthetic carbon fixation was within 10% of being directly proportional to light energy in Brooks Lake, Alaska, on a cloudy and a bright day in August, 1957. Where considerable variation in light intensity occurs it is difficult to make a valid estimate of primary productivity in lakes on the basis of occasional measurements. Where light conditions are more uniform the frequency of measurement can be reduced without serious loss in precision. In the summer of 1961 a series of primary productivity measurements for sixteen consecutive days were made by the author in Castle Lake, California. By comparing the average of these measurements with the averages of those measurements taken every fifth day through the series, an estimate of the loss of precision in using a five day sampling schedule was obtained. The mean of the

five comparisons was 7.6% with a maximum error of 22% if only the three cloudy days in the series were considered. Photosynthesis in relation to light intensity has been under investigation for many years (Manning et al., 1938; Manning and Juday, 1941; Edmondson, 1956). The measurable interaction between primary productivity and the optical qualities of water have led Vollenweider (1962) to characterize lakes on this basis. The pattern of light at various depths may be used to predict the primary productivity.

The importance of making continuous light measurements in primary productivity studies can scarcely be overemphasized. Unless measurements are made every day, or happen to hit average light conditions, estimates of productivity may be greatly in error. Either a photocell or pyrheliometer can be used to record light conditions. The solar radiation can conveniently be expressed in energetic terms by using the Langley per minute (15°C gram calorie per cm^2 per minute). By applying a correction factor of 0.5, the Langley per minute can be converted to the photosynthetic portion of the spectrum (3800–7200 Å) (Strickland, 1958). Recording pyrheliometers make continuous light measurements in the field possible.

The number of samples used to describe the vertical distribution of photosynthesis in lakes has been as variable as the environments themselves. In general when an oligotrophic lake is studied for the first time the euphotic zone should be covered with a sample every meter through the thermocline with five meter intervals below. It is unlikely that the euphotic zone will extend more than 3.5 to 4 times the Secchi depth. Four or five dark bottles at 5 to 10 meter intervals should be adequate to estimate non-photosynthetic carbon uptake. This carbon accumulation in the dark may result from chemosynthesis (Kuznetsov, 1956), adsorption to outer plant space (Kramer, 1957), or the Wood-Werkman reaction (Steemann-Nielsen, 1960a). Inclusion of an initial pre-filtered (Millipore) control may also be advisable to be certain that inorganic precipitation of carbon-14 is not occurring (Goldman and Mason, in press). In marl lakes, where precipitation can result from the photosynthetic activity, controls of this sort may be of limited value, although acid should readily remove the precipitate. In more eutrophic waters, with reduced euphotic zone, fewer samples are required, but they should be placed at about ½ meter intervals. On the basis of high initial sampling, reduction in the number of samples can be made in the straighter portions of the photosynthetic curve. Where radical reduction in sampling is necessary, a depth such as the 1-2 m strata in Lake Erken (Rodhe et al., 1958) may give a fairly constant proportion of the total production per unit of surface area.

(2) Field Equipment. The importance of using non-metallic water samplers is discussed by Doty and Oguri (1958) and the necessity of preventing bacterial growth on the walls of plastic samplers is evidenced by Holmes (1958b). Inhibition of photosynthesis by contact with metals appears to be the rule in salt water. In Lake Tahoe, a freshwater lake, Goldman (unpublished) has found that a brass Kemmerer water bottle actually stimulates the rate of carbon fixation. After the addition of sodium carbonate to a thoroughly mixed sample of Lake Tahoe water, half was poured into a clean Kemmerer water sampler. At timed intervals, 125 ml samples were withdrawn from the darkened polyethylene container and from the Kemmerer bottle and incubated for four hours before filtration through an HA Millipore filter. The HA filters from water which had metallic contact for 2 minutes showed a 10% increase in carbon fixation, while the sample which had an 8 minute contact gave an 11% increase.

Some equipment useful to facilitate rapid sampling is shown in Figure 2. Opening ampules is a rather slow process in comparison to continuous pipetting with an automatic hypodermic syringe. Stock solutions may be removed from a serum bottle by connecting the pipetting hose to a hypodermic needle and venting the bottle with a second, cotton-plugged needle. A better method is to use a large syringe like the 100 ml size pictured, for a sterile reservoir. This has the advantage of sterile transfer without any air space for CO_2 exchange. This syringe should be protected from solar heating. The sample box is fitted with an inner, sliding cover so that bottles need not be exposed to daylight each time new samples are added. The exterior of the box is painted white to reduce solar heating. The dark bottles to be placed near the surface should be painted white for the same reason. A small piece of bicycle inner tube will conveniently serve as a light seal between the dark bottle and its taped glass stopper. Aluminum rods or wire can be used to suspend a dark and light bottle at a particular depth to prevent breaking the bottles or shading the sample.

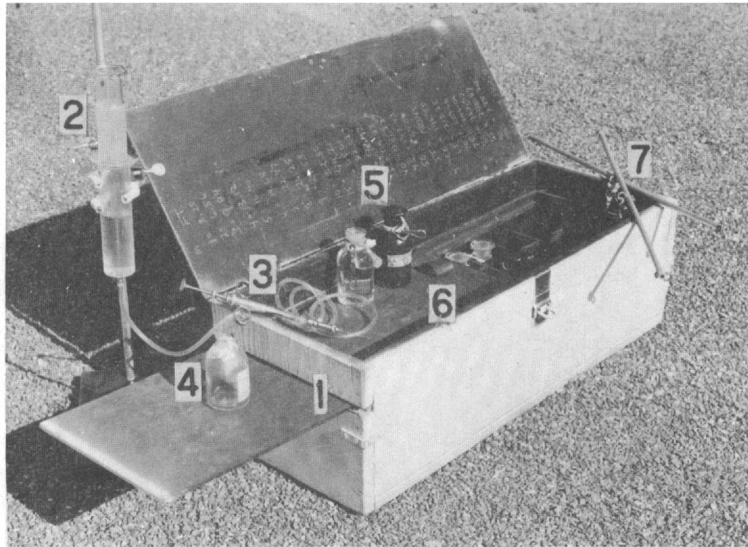

Figure 2 — Field equipment for the carbon-14 primary productivity method. 1: Opaque box, with sliding inner panel; 2: large (100 ml) syringe for sterile carbon-14 reservoir; 3: automatically refilling injection syringe; 4: initial sterile carbon-14 stock bottle; 5: light and dark bottles; 6: opaque sleeve to fit over the glass stopper of dark bottles; 7: separator for suspending bottles at same depth.

(3) Incubation time and diurnal studies. The length of time between the addition of carbon-14 and the filtration of the samples has varied with different workers: 48 hours (Frey and Stahl, 1958; Ichimura and Saijo, 1958; Vinberg and Kaler, 1960); 24 hours (Kuznetsov, 1955 and 1956; Fogg, 1958; Frey and Stahl, 1958; Ichimura and Saijo, 1958; Rodhe, 1958a and 1958b; Rodhe et al., 1958; Vinberg and Kaler, 1960); 12 hours (Sorokin, 1959); 6 hours, or noon to sunset (Ichimura and Saijo, 1958; Steemann-Nielsen, 1958c and 1959; Jonasson and Mathiesen, 1959; Vollenweider, 1960); 4 hours (Goldman, 1960a). The most definitive work on the subject was done by Vollenweider and Nauwerck (1961) who compared 4, 8, 12, 16, and approximately 20 hour incubations. In comparing the sum of 8 hour experiments with the sum of short (4 hour) experiments they found that the longer incubation time resulted in a deficit of 21% for a day. Further, there was considerable variation in this deficit with depth. They concluded that 3-6 hour experiments give reliable results. A half day's incubation (Steemann-Nielsen, 1958c and 1959; Jonasson and Mathiesen, 1959) or the noon to sunset experiments of Sorokin (1959) were doubled to estimate a day's photosynthesis. Vollenweider and Nauwerck (1961) note that this procedure fails because photosynthesis is asymmetrical in relation to the insolation curve. Ohle (1961) has observed distinct maxima and minima in photosynthesis during a day with higher rates in the morning.

A more accurate method of estimating a day's photosynthesis is by making one or more diurnal studies during the field season (Goldman, 1960a). Four to six hour measurements can easily be converted to daily estimates by comparison of the area beneath these curves, and slight variations in incubation times from day to day are accounted for more accurately on this basis. Two or three diurnal studies (samples changed every four hours from dark to dark) have been made by the author yearly since 1959 at Castle Lake, California. Using diurnal studies made in June, July, August, and September, comparisons were made between two times half a day's carbon fixation and the total for the day. Doubling a half day's measurement would have resulted in overestimates of 10, 7, 13, and 8% for these months. The values reflect a lack of any great variation in photosynthesis between morning and afternoon in this rather transparent (Secchi depth 10-12 m) cirque basin lake.

(4) Light inhibition. Exposure of samples to surface light should be avoided. During winter studies at Castle Lake, California (Goldman, 1961b), samples taken to a depth of 5 m beneath the ice which were exposed to direct sunlight showed significantly lower carbon fixation

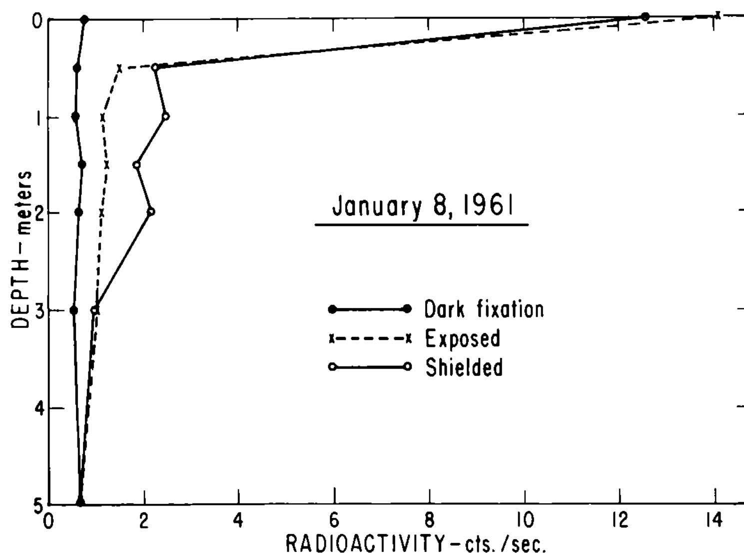

Figure 3—Inhibition of carbon fixation in samples exposed to direct sunlight before a four-hour in situ incubation under ice cover in Castle Lake, California.

than parallel samples which had been protected from light by enclosure in black sacks during $Na_2C^{14}O_3$ addition (Fig. 3). Because of the great sensitivity of the isotope method, protecting samples from surface light is recommended by Sorokin (1959). The reduction of photosynthetic rate so frequently observed near the surface (Manning and Juday, 1941; Edmondson, 1956; Talling, 1957 and 1960) is certainly rather complex in character (Kok, 1956), and it is uncertain how this inhibition may be related to ultraviolet light (Manning et al., 1938; Holt et al., 1951; Gessner and Diehls 1951; McMillan and Verduin, 1953) or extreme-red light (Rabinowitch et al., 1960; Govindjee et al., 1961).

(5) A standardized field procedure. In view of the foregoing remarks on present methods and variations in field procedures, it would seem desirable, without being excessively rigid, to suggest a standard procedure for the in situ measurement of primary productivity in freshwaters based on the review of present methods. For the most part these are the methods which have had the greatest general acceptance. Ex situ studies (referred to by some workers as in vitro) will not be further discussed, as they rely on in situ measurements for evaluation.

(a) $Na_2C^{14}O_3$ solution: made up in single large lot with minimum carrier and dilution to 2-5 microcuries/ml with de-ionized, glass distilled water; pH adjusted to 9.5 or below for very soft waters; ampulated and autoclaved or packaged in sterile serum bottles with thick CO_2 impermeable stoppers; absolute activity determined by gas phase or liquid scintillation counting.

(b) Sampling equipment: non-metallic water sampler; 125 ml pyrex bottles with ground glass stoppers; dark bottles covered with black tape and checked for light leaks; snaps at neck for rapid attachment to rings on metered incubation line; automatic syringe for 1 ml carbon-14 addition to samples; spreaders to keep dark and light bottles at same depth; floating station with counter-weighted boom to prevent sample shading; light recording equipment.

(c) Field procedure: one ml of carbon-14 solution/125 ml of sample; incubation for 4 to 6 hours during the middle of the day or, if diurnal curves show good symmetry and day length does not exceed 12 hours, half day incubation. In the former, more desirable method, daily productivity should be based on the diurnal curves; exploratory sampling to determine the necessary number of stations and number of samples per station; sampling to mean depth or 4 times Secchi depth (whichever value is smaller); samples collected from surface down; all samples in light tight box before carbon-14 addition; dark bottles included at least every five meters with all in situ experiments; gravimetric, gasometric, gas-diffusion, or conductivity check on total carbon determination if it is based on pH and total alkalinity; at least one duplicate run during the study for estimating experimental error.

(d) Filtration: on 0.5μ membrane or 0.45μ HA Millipore filters at 15 inches Hg vacuum; immediate rinse with 5 ml 3% formalin; .003N HCl rinse only if inorganic precipitation is indicated. Volume filtered inversely proportional to algal density, and filtration time as influenced by filtration area; air dried before storage in CO_2 free evacuated desiccator with ring weight to prevent filter curling.

(e) Counting: by G.M. thin window gas flow counter whose efficiency is based on the absolute activity of an algal source; after counting the source with the G.M. unit, it should be converted to CO_2 and its absolute activity determined by the gas phase or scintillation methods already discussed.

(f) Results: expressed as approximate net photosynthesis in both mg C/m^2/day and mg C/m^3/day, and computed from planimetry of the vertical distribution of photosynthesis minus dark uptake. Inclusion of a 6% correction for isotope effect still appears a reasonable correction.

3. BIOASSAY OF LIMITING FACTORS WITH CARBON-14

Justus Liebig's (1849) "law" of the minimum has been applied in many areas of biology where there has been considerable interest in determining what chemical factors limit the productivity of environments. The over-simplification of Blackman's concept of a single limiting factor is discussed by Verduin (1952a). In addition to the variety of macronutrient requirements, trace element deficiencies are clearly evident from bioassay studies in both plants (Arnon, 1958a and 1958b; Hewitt, 1959) and animals (Underwood, 1958). Extensive culturing of algae, leading to the isolation of growth factors, has been a frequent approach (e.g. Chu, 1942; Rodhe, 1948; Provasoli and Pintner, 1953; Arnon, 1958b). The extensive work in this area has contributed a great deal to our knowledge of algal nutrition, and has been reviewed by Lund and Talling (1957).

Bioassays of natural waters for factors limiting plant growth have been rather less common than similar experiments with terrestrial plants. Although the geology and geochemistry of an area can provide important insight into limiting factors, a host of other variables affect the availability of nutrients. A lake or river is a collecting site for the variety of ions which provide the basic nutrient substrate for the primary producers. As such it is an integrated solubility complex of all the substances in the rain water, of all the elements leached from the watershed, and of all the ion exchange activities associated with the soil through which it passes. Pond and lake water has been used as the culture medium under laboratory conditions with various nutrient regimes and algal inoculations by Strøm (1933), Fish (1955b), Potash (1956), Eyster (1958), and MacPhee (1961). Lake waters with their natural populations have been cultured by Nelson and Edmondson (1955), and Goldman (1960a and 1960b).

Most studies have relied on cell counts, extinction coefficients, chlorophyll, or other general indices for changes in standing crop. These measurements of standing crop require long culturing periods which may result in development of an unnatural population balance as evidenced by the early work of Whipple (1896). The oxygen method has been used to measure growth in cultures in fertilized salt water by Edmondson and Edmondson (1947), and by Goldman (1960a) as a check on in situ carbon-14 bioassay of limiting factors in Alaskan lakes. The high sensitivity of the isotope method makes changes in photosynthetic rate detectable within minutes after the addition of limiting nutrients (Goldman, 1960a). This method has been applied successfully to marine studies by Ryther and Guillard (1959) and Menzel and Ryther (1961a).

a. Laboratory methods for carbon-14 bioassay

An extensive literature on culture techniques exists and has recently been assembled by Lund and Talling (1957). In general the actual establishment of cultures using carbon-14 differs little from the older methods. Since the assay technique is considerably more sensitive than older methods, the greatest possible care should be exercised in preparation of the carbon-14 solution used in assay, the nutrient additives, and the culture containers. Preparation of the carbon-14 is discussed in 2,a.(2) of this paper. The nutrient solutions should be prepared of the best available, and in some cases repurified, reagents. To isolate limiting

factors, a variety of nutrients can be prepared so that the same elements are balanced in one or more different compounds. The use of much higher than naturally occurring concentrations of nutrients should be discouraged as this may actually add trace element impurities in sufficient quantities to stimulate growth. Some of the rather high optimal levels of addition quoted in the development of culture media may reflect growth stimulation from such impurities. All nutrients should be sterilized and in the case of iron and certain vitamins be prepared just prior to their use. Rodhe (1948) and Provasoli et al. (1957) discuss preparation of nutrient media.

Major sources of experimental error are: Inaccurate nutrient and carbon-14 addition, lack of homogeneity in culture media, and inadequately cleaned culture containers. The carbon-14 label can be added separately to each subsample of the culture, separately to each of the cultures, or to the entire culture medium before division into the various culture flasks for nutrient addition. The last method has the distinct advantage of eliminating the carbon-14 measuring error between cultures with a single isotope addition for the entire experiment. The first method, used principally by the author in Alaskan studies (Goldman, 1960a), allows larger culture volumes with only a small carbon-14 label added for the incubation of subsamples. If polyethylene containers are used for culture (e.g. McAllister et al., 1961; Goldman, 1962) this subsampling should be done in glass, as CO_2 is exchanged rather rapidly through the plastic. Starting with the same initial activity, after four days incubation in Castle Lake cultures in plastic bags retained only 10% as much activity as cultures of the same volume in pyrex flasks (Goldman unpubl.). The second method is justified only where the entire culture medium cannot be collected in a single mixing container. The lack of uniform plankton distribution in surface water (Cassie, 1958) favors mixing the total culture medium thoroughly before distribution to the culture containers. Nutrient solutions should be prepared so that the volumes added are adequate to insure a high degree of accuracy in their volumetric addition. Special care should be taken in cleaning the glassware. Steam cleaning and autoclaving all culture flasks give better results than just autoclaving. Rinsing about seven times in the lake water to be assayed is also recommended.

Containers of liter or half liter size are preferable to smaller volumes, as they reduce the surface to volume ratio, and allow more precise nutrient addition. Screw cap Erlenmeyer flasks have been used in both laboratory and field culturing. Both dark and Millipore filtered control cultures are recommended where inorganic precipitation may occur (Goldman and Mason, in press). A large size polyethylene jug is convenient for collecting the culture water and mixing in the added carbon-14.

b. In situ cultures

Carbon-14 provides a rapid and convenient means of field assay for nutrient limiting factors under a variety of natural conditions. Goldman (1960b) has had measurable response in Castle Lake, California with the addition of a few parts per billion molybdenum to cultures of the natural plankton population under a meter of ice. Cultures may be maintained in a partially submerged crib with surface light and temperature conditions (Figure 4) or at various depths by attachment to a float. The latter method can easily be used at primary productivity stations during the regular incubation periods. Any wave motion will tend to keep the plankton in suspension in either situation. One of each duplicate sample taken at various depths can have nutrient addition while the other serves as a control and the standard in situ primary productivity measurement. This kind of experiment serves to indicate the extent of nutrient limiting factors with depth.

If the entire water column is to be isolated by the "plankton shaft" of Pettersson et al. (1939), the Plankton-Test-Lot of Thomas (1958), or the polyethylene film cylinder of Goldman (1962), nutrients can be mixed into the entire water column. Subsamples from inside the water column can then be incubated with carbon-14 addition in the lake at appropriate depths. Under these conditions water from outside the cylinder can serve as a control. The high sensitivity of the carbon-14 tracer can thus be brought to bear on the complicated interactions of the aquatic ecosystem. Any change in carbon fixation initiated by addition of deficient elements or inhibiting substances can be detected with a high degree of precision.

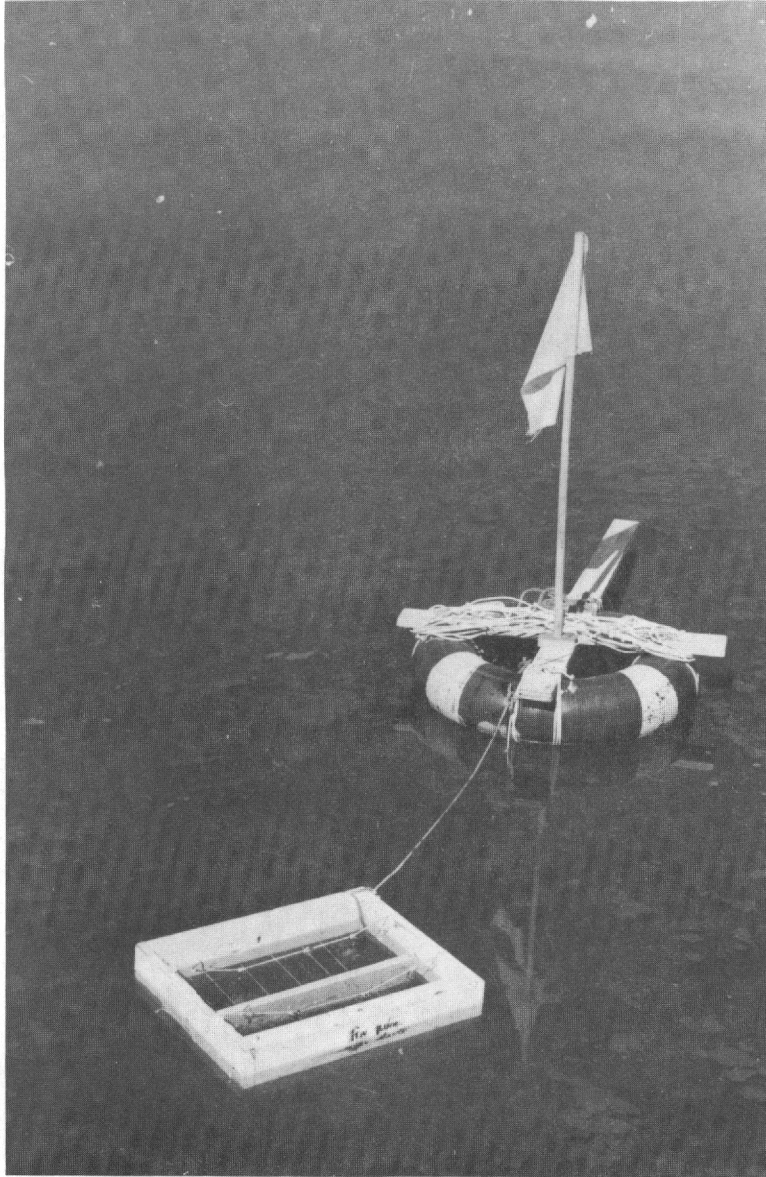

Figure 4 — Culture crib for incubation at surface light and temperature conditions in Clear Lake, California.

THE STANDARDIZATION AND COMPARISON OF MEASUREMENTS OF PRIMARY PRODUCTION BY THE CARBON-14 TECHNIQUE

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ABSTRACT

A prerequisite of measurements of primary production by the carbon-14 technique and their comparison is the reliable standardization of the amount of carbon-14 added to the sample. This Added Activity must be determined under conditions identical with the Geiger counting of the phytoplankton samples, i.e., with the same counting geometry and at zero-thickness.

In most of the carbon-14 techniques described, self-absorption curves are prepared from the Geiger activities of $BaCO_3$ planchets of varying thicknesses containing aliquots of the Added Activity. These curves are then extrapolated to zero-thickness either empirically or mathematically.

The empirical extrapolation suffers from two important disabilities; the subjective nature of the curve and the difficulty of preparing thin planchets of $BaCO_3$. The mathematical extrapolation is easier and not subjective but gives large errors as the curve follows neither an exponential nor a hyperbolic function. Attempts to prepare thin planchets show that the curve becomes complex as it approaches zero-thickness, due to the increasing importance of back-scattering of the β particles.

Whilst both empirical and mathematical extrapolations can lead to large errors in the estimates of Added Activity at zero-thickness they can be made highly reproducible. This can be checked by the use of estimates of the zero-thickness activity of standard carbon-14 solutions. This allows the reliable comparison of results obtained with the same counting equipment but not of those from different instruments.

A new method has recently been described which consists of determining the absolute activity of the carbon-14 added and the efficiency of the Geiger counter at zero-thickness and hence the Added Activity. This is done by Geiger counting extremely thin films of plastic labelled with carbon-14 and then determining the absolute activities of both the films and the Added Activity by liquid scintillation counting. This method is direct, objective, and simple but requires special equipment. It shows that extrapolations of self-absorption curves can lead to errors of about 20%.

Most of the measurements of primary production in the Pacific Ocean have been made by various adaptations of the techniques of Steemann-Nielsen, Sorokin, Doty, and Jitts. The first two measure net daily production under conditions of natural daylight variation, while the second two measure relative productivity under conditions of constant artificial illumination. In the technique of Sorokin relative productivity is measured as a preliminary step to obtaining net production. Any attempt to compare the results of the first two techniques to those of the second two, would require the establishment of suitable factors relating them.

A direct comparison of the results of two different techniques has been made only for those of Doty and Jitts. This was done by adjacent sampling by the two techniques but using the same Added Activities and Geiger equipment for both techniques. The correlation between the results was significant at better than the 5% level.

I. INTRODUCTION

The carbon-14 technique for measuring the primary production of organic matter in the oceans, first described by Steemann-Nielsen (1952), has been widely used by many workers in the Pacific Ocean. Almost every one of these workers has introduced small or large innovations in the technique. Before the many results which are now available can be compared, it is necessary to assess the implications of these innovations. As an example, the carbon-14 technique is being used by different workers to estimate variously, gross daily production, net daily production, and relative productivity. Most of these results are published as measurements of primary production.

Apart from the differences in the end-product of measurements, the various techniques also differ considerably in the equipment and methodology used. In this review an attempt is made to compare the main differences of the more widely used techniques. As far as possible, the terminology of Strickland (1960) is adopted.

A prerequisite of measurements of primary production, to enable their comparison to be made with any confidence, is the reliable standardization of the amount of carbon-14 added to each sample. The work of Doty (1959a) and Jitts and Scott (1961) has demonstrated that this can be a source of considerable errors. For this reason the subject of standardization of carbon-14 solutions will be dealt with in greater detail than others.

II. STANDARDIZATION

The measurement of primary production using carbon-14 is essentially an isotope dilution technique and the results are given by the equation (Doty, 1956):

$$\text{Production} = \frac{\text{Net Activity}}{\text{Added Activity}} \times \frac{\text{Concentration of total } CO_2}{\text{Period of Incubation}}$$

where Net Activity is the Geiger activity of the phytoplankton due to photosynthetic uptake of carbon-14 and Added Activity is the Geiger activity of the known amount of carbon-14 added to the sample prior to its incubation in light. The Net Activity of the phytoplankton is usually measured by filtering them from the sample onto a membrane filter and counting with an end window or windowless Geiger counter. As the amount of phytoplankton on the filters is usually less than 0.1 mg/cm^2 (Strickland, 1960) it is assumed that self-absorption of the carbon-14 β particles by the phytoplankton is negligible, i.e., that the activity is measured at zero-thickness. To obtain the ratio Net Activity/Added Activity it is essential that the two activities be directly comparable, i.e., that the Added Activity be estimated for the same conditions of geometry and back-scattering in the counter and at zero-thickness.

A method has been described for the direct measurement of the Added Activity by drying a small aliquot of the carbon-14 stock solution on a planchet and counting it in the same way as the phytoplankton (Anon, 1960). However, this method can give only an approximate measure of the Added Activity due to the liability of the $NaHC^{14}O_3$ when dried (Strickland, 1960).

Miyake et al., (1954) describe a method in which both the labelled phytoplankton and aliquots of the Added Activity are converted to gaseous $C^{14}O_2$ and their activities determined in a gas counter. This method certainly gives directly comparable activities, but the techniques are exacting and time-consuming. As such they are not suitable for widespread use.

(a) The extrapolation of self-absorption curves

In most of the carbon-14 techniques described, the Added Activity is determined indirectly

from self-absorption curves of $BaCO_3$ planchets of varying thicknesses prepared from aliquots of the carbon-14 stock solutions. The methods of preparation of the planchets have all been adapted from those described by Calvin, et al., (1949). The Added Activity is obtained by extrapolating these self-absorption curves to zero-thickness. The extrapolation can be done empirically (Steemann-Nielsen, 1952; Doty, 1956 and 1959a; Thomas, 1959) but the accuracy is limited by the difficulties of obtaining planchets of thicknesses in the critical range of less than 0.5 mg/cm^2 (Jitts and Scott, 1961). A major criticism of these methods is the subjective nature of the extrapolation.

To avoid the difficulties of preparing very thin planchets and the subjectivity of empirical curves, the extrapolation has been made mathematically. To do this, self-absorption has been assumed to follow an exponential function (Jitts, 1957; Anon, 1960) or a hyperbolic function (Hendler, 1959). Whilst these methods can be highly reproducible, they give results which can be as much as 20% low. There is evidence that this is caused by the failure of the self-absorption curve to follow either an exponential or a hyperbolic function at thicknesses less than 1 mg/cm^2 due to back-scattering of the β particles at these thicknesses (Anon, 1960; Jitts and Scott, 1961).

The reliability of any particular method of extrapolation of self-absorption curves can be checked by the method of Berson and Yalow (1960). In this, aliquots of a standard solution of carbon-14 of a known absolute activity are added to replicate aliquots of the unknown carbon-14 stock solution. The increase in activity of the planchets with the standard solution over those without the standard, when divided by the known absolute activity of the standard, gives the fraction of the absolute activity measured by the counting system under the specified conditions of self-absorption. When the activity of the planchets without the standard is divided by this fraction, the absolute activity of the unknown carbon-14 stock solution is obtained. Whilst this does not help in obtaining the zero-thickness activity of the carbon-14 stock solution unless the efficiency of the Geiger counter is known, it permits the reproducibility of the method to be determined.

The above considerations show that the use of extrapolations of self-absorption curves can be made to be highly reproducible but that considerable inaccuracies can be introduced. This means that whilst these methods can be used for relative measurements of primary production with the same Geiger counter, they can measure zero-thickness Added Activities only with a limited accuracy. This can introduce considerable error when measurements of primary production using different Geiger counters are compared.

(b) The scintillation counting method

A method for determining the Added Activity at zero-thickness has been recently described (Jitts and Scott, 1961) using liquid scintillation counting. In this method the absolute activities of the carbon-14 stock solutions are determined by comparing their activities with those of a known quantity of carbon-14 standard solution. The zero-thickness Geiger efficiency of the counter used for measuring the Net Activity of the phytoplankton is determined by first Geiger counting several thin films of carbon-14 labelled plastic mounted on membrane filters identical with those used in filtering the phytoplankton. These films are then dissolved in some liquid scintillator and their absolute activities are determined again by comparison with the carbon-14 standard solution. The ratio of the Geiger activity to the absolute activity of these films gives the efficiency of the Geiger counter. Knowing the absolute activity of the carbon-14 stock solution and the efficiency of the Geiger counter, the Added Activity can be calculated directly.

A significant feature of this method is that the efficiency of the Geiger counter is determined under conditions closely resembling those used for counting the labelled phytoplankton. The films of plastic have thicknesses and densities of the same order as those of the phytoplankton, and thus the self-absorption of particles can be claimed to be negligible with equal justification. For the same reasons and because the films are spread with the same geometry over identical backing material, i.e., membrane filters, it can also be assumed that back-scattering of the β particles is similar for the films and for the phytoplankton. The importance

of these considerations has been demonstrated in the previous section on the preparation of thin planchets of $BaCO_3$ for determining self-absorption curves.

Jitts and Scott (1961) determined the efficiency of the Geiger counter used as 58%. More recent work (unpublished) suggests that this value was too high, the correct value being about 50%. This was caused by the inaccuracy of the value used for the absolute activity of the carbon-14 standard solution. However as both the Geiger efficiency and the absolute activities of the carbon-14 stock solutions are obtained by reference to the same carbon-14 standard solution, the values and accuracy of the determination of the zero-thickness Added Activities are not affected.

With the cautionary note that it is advisable to use the same carbon-14 standard in determining both the Geiger efficiency and the absolute activities of the unknown carbon-14 stock solutions, it is felt that the scintillation method gives reliable determinations of the Added Activity and hence of primary production which would allow direct comparisons of results obtained with different Geiger counters and carbon-14 stock solutions. Whilst this method does require the use of special equipment, it is direct, objective, and comparatively simple.

III. THE COMPARISON OF CARBON-14 MEASUREMENTS

Most of the measurements of primary production in the Pacific Ocean have been made by various adaptations of the techniques of Steemann-Nielsen (1952), Sorokin (1956), Doty (1956), and Jitts (1957). If any attempt is made to compare results obtained by these techniques, it is necessary to consider the differences in methods and equipment used by them as well as the nature of the results presented.

No attempt will be made here to deal with all the various adaptations, nor will any particular method be examined exhaustively. The subject has been recently reviewed by Vinberg (1960) and Strickland (1960). Only the main differences of the four techniques mentioned will be compared. These have been summarized in Table 1.

(a) Sampling depths

Steemann-Nielsen (1952) takes samples from depths to which selected percentages of surface light penetrate, usually surface, 10% and 1%. In the technique described by Sorokin (1956) depths are selected arbitrarily, usually 0, 10, 25, 50, 75, 100, 150, and 200 m, and are varied to suit such conditions as can be determined or predicted, e.g., the depth of the thermocline and the euphotic layer, (Anon, 1960). Most of the results reported using the technique of Doty (1956) have been for surface samples only, though several workers (e.g., Angot, 1960; Ichimura and Saijo, 1959) have taken samples from fixed arbitrary depths. In the technique of Jitts (1957) samples are taken from fixed arbitrary depths, usually 0, 25, 50, 75, 100, and 150 metres below the surface.

(b) Light Incubation

In the technique of Steemann-Nielsen (1952) samples are either incubated in situ, e.g., resuspended at the depths from which they were taken, for a whole or a half daylight period, or in a bath with constant artificial light (18,000 lux).

In the technique of Sorokin (1956) samples are incubated in situ or alternatively a surface sample is incubated in a barrel exposed to natural sunlight whilst others from various depths are incubated in a light bath with a constant but unspecified light intensity.

In the techniques of both Doty (1956) and Jitts (1957) samples are incubated in a light bath with constant light intensities of between 900 and 1100 ft candles. The Jitts (1957) technique has also been used with in situ incubation (e.g., Dyson 1958; Angot, 1960).

(c) Dark Uptake of Carbon-14

Steemann-Nielsen (1956) measured the dark uptake of carbon-14 on occasional samples to determine a percentage correction, usually 1 or 2%. In the Sorokin (1956) technique it is not made clear whether or not dark uptake is measured, though a later publication (Anon, 1960)

Table 1 — Comparison of Differences in Four Carbon-14 Techniques of Measuring Primary Production

Technique	Selection of Sampling Depths	Method of Incubation	Results Obtained	Dark Uptake Measurements	Geiger Counter	Solution Standardization	Isotope Effect Correction	Respiration Correction
Steemann-Nielsen (1952)	Percentages of surface light	*In situ* and light bath	Gross daily production	Occasional to determine correction	End window	Empirical extrapolation self-absorption curve	Yes	Yes
Sorokin (1956)	Variable Arbitrary	*In situ* and light bath	Net daily production	Occasional plus *in situ* below euphotic layer	End window	Empirical extrapolation of curve	No	No
Doty (1956)	Surface	Light bath	Relative productivity	With each sample	Windowless	Empirical extrapolation of curve	No	No
Jitts (1957)	Fixed Arbitrary	*In situ*	Net daily production	With each sample	Before 1958 End window	Before 1959 Exponential extrapolation of curve	No	No
		Light bath	Relative productivity		After 1958 Windowless	After 1959 Liquid scintillation counting		

stresses the importance of this measurement and describes a method in which samples are suspended well below the euphotic layer to determine the necessary correction for both dark uptake and uptake during handling. The techniques of both Doty (1956) and Jitts (1957) require the measurement of dark uptake on replicates of each sample taken.

(d) Geiger Counting

An end-window counter is used by Steemann-Nielsen (1956). It is stressed that samples should have activities at least 10 times background and that all counts are standardized against an elemental carbon-14 standard (Steemann-Nielsen and Aabye-Jensen, 1957). Geiger counting in the Sorokin (1956) technique is done with an end-window counter (Anon, 1960) but no further details are given. In the technique of Doty (1956) samples are counted with a windowless counter for up to 10 minutes to obtain about 1000 counts if possible. All counts are standardized against a plastic carbon-14 standard. In the Jitts (1957) technique an end-window counter was used prior to 1958, but thereafter a windowless counter was used. All counts are taken to five minutes and standardized against a plastic carbon-14 standard.

(e) Standardization of carbon-14 solutions

The technique of Steemann-Nielsen (1952) uses empirical extrapolation of self-absorption curves of $BaCO_3$ planchets varying in thickness from about 1 to 20 mg/cm^2. For the Sorokin (1956) technique various methods are described (Anon, 1960) but the exponential extrapolation of the self-absorption curve appears to be most favoured. The Doty (1956) technique also uses the empirical extrapolation. The Jitts (1957) technique used exponential extrapolation until 1959 when the liquid scintillation counting method (Jitts and Scott, 1961) was adopted.

(f) Correction for Isotope Effect

Only the Steemann-Nielsen (1956) technique makes a correction for isotope effect, using a value of 5%. In the Sorokin technique no correction is made (Anon, 1960) though the later work of Sorokin (1959) suggests that the value should be 6.79%.

(g) Nature of the results presented

The results presented by the Steemann-Nielsen (1952) technique are for gross daily production per square meter of sea surface as measured in situ for the conditions of sunlight and submarine light penetration pertaining on the particular day of the measurement. This is obtained with the use of an overall correction factor of +10% to account for respiration, dark fixation and isotope effect. For results obtained in the constant light bath an empirical formula is used again to calculate gross production per m^2.

The Sorokin (1956) technique gives results of a similar nature to the above. However as no corrections are made for respiration these results represent measures of net daily production. When the Jitts (1957) technique is used for in situ measurements, the results also represent net daily production.

Apart from considerations of differences in sampling depths, standardizations, and applied corrections, the in situ measurements of the Steemann-Nielsen, Sorokin and Jitts techniques are of a comparable nature. Although no experimental comparisons have been reported, it is unlikely that these differences would lead to variations of more than 50% in replicate measurements by these three techniques.

In the light bath techniques of Doty (1956) and Jitts (1957) the results represent measures of relative productivity, i.e., the rate of photosynthetic uptake of CO_2 by the samples when exposed to a constant artificial light. As the light intensities used in the two techniques are similar their results are directly comparable. Neither technique uses corrections for isotope effects or respiration, but use different methods of sampling and carbon-14 standardization.

The light bath measurements made with the Steemann-Nielsen technique are also of a comparable nature to those of Doty and Jitts, except that corrections are made for respiration

and isotope effect. In the indirect measurement of net daily production by the Sorokin technique, light bath incubation is also used but the light intensity is not specified.

The measurements of gross and net daily production obtained by the in situ techniques of Steemann-Nielsen, Sorokin, and Jitts cannot be compared with the relative productivity measurements of the light bath techniques of Doty and Jitts without applying factors to relate the two measurements. These factors would depend upon both solar and submarine light conditions at the time of measurement, and on the relations of photosynthesis by the samples to variations in light intensity. They will therefore vary from one region to another and also from day to day. In the Steemann-Nielsen technique relative productivity is converted to daily production by means of an empirical formula. In the Sorokin technique this is done by experimentally determining the factor for daily solar variations with each measurement and the factors for submarine light and photosynthesis vs light intensity from time to time when possible. In the Jitts technique the relative productivity per hour per m^2 of sea surface is multiplied by the arbitrary factor of ten, but this can only be regarded as a means of obtaining a result with a similar order of magnitude to that of daily production.

(h) The experimental comparison of different techniques

The experimental comparison of two different techniques has been reported only for those of Doty (1956) and Jitts (1957). As part of a joint project by the University of Hawaii and C.S.I.R.O. Australia, the two techniques were compared during Cruise 43 of the "Charles H. Gilbert" (Doty, 1959a). Duplicate measurements were made on surface samples taken within a few minutes of each other by the two techniques. To reduce the number of variables, the same Added Activity and Geiger equipment were used for both techniques. The pairs of results were closely similar, having a correlation coefficient of 0.960 which was significant at the 5% level. The results of the Doty technique were about 20% higher than those of Jitts. Experiments to assess the reasons for this were not conclusive but the difference in light intensities in the incubators may have been responsible.

Angot (1960) reports a similar experimental comparison as above. However he failed to find a significant correlation between the results of the two techniques. One reason for this may have been that half of the results he used were made with a faulty carbon-14 stock solution.

PHYTOPLANKTON PIGMENTS IN THE PACIFIC OCEAN

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INTRODUCTION

In this review an attempt is made to summarize what is known of the distribution of phytoplankton pigments in the Pacific Ocean. To do this adequately, it has been necessary to describe the analytical methods used and to refer occasionally to work done in other oceans.

The pigments in phytoplankton are mainly chlorophylls and carotenoids. Their occurrence in the different classes of algae is shown in Table 1 which is adapted from Smith (1951).

In studies on primary production chlorophyll-a has received more attention than any other pigment. The amount of -a in a water-sample has been used as a measure of its photosynthetic potential, i.e., it has been observed that under certain sets of conditions (temperature, light, etc.) the amount of production is proportional to chlorophyll-a concentration (Ryther, 1956b). The amount of -a has also been used as a measure of the amount of phytoplankton (standing stock, Cushing et al., 1958) and thus as a basis for comparing rates of primary production. Examples of these uses are the investigations of Ryther and Yentsch (1957) who found that 3.7 mg C were fixed per mg chlorophyll-a per hour and of Harvey (1950) and Riley (1955) who calculated organic matter from pigment content. More recently, Shimada (1958), Doty (1961), and Jitts (unpublished) have calculated the correlations between production (mg C fixed) and pigments (chlorophyll-a, -b, -c, astacin and non-astacin types).

The use of chlorophyll-a for estimating standing stock has the disadvantages that the concentration of -a is not constant from one species to another, that it is not constant throughout the life-cycle, and that it is not constant on a daily or seasonal basis. The disadvantages of using the amount of -a as an index of photosynthetic potential arise from the facts that -a is not the only pigment which absorbs light whose energy is used for photosynthesis, and that there are no field methods for measuring the proportion of the total -a which is photosynthetically active at a given time. Currie (1958) used total plant pigment (chlorophyll a + b + c + plant carotenoids) and found that "the agreement between carbon fixation and 'photosynthetic potential' was not so good when chlorophyll-a alone was used as the measure." However, since it is not known what the agreement should be, it is not possible to accept Currie's conclusion.

Despite these disadvantages, many estimations of chlorophyll-a (and other pigments) are made. The disadvantages are slowly being overcome as more knowledge is gained and it is probable that pigment determination, rather than cell counts, cell volumes, dry weight, or total nitrogen, offers the best hope for a field method for standing stock of phytoplankton.

The relation between pigments and photosynthesis is not sufficiently clear to allow photosynthetic potential to be calculated from pigment content. In fact it may not be possible to make such a calculation. However, it is necessary to elucidate the relation in order to understand the processes involved in biological production.

Annotated Bibliography for the Pacific Ocean

The work carried out in the Pacific Ocean is summarized in the charts included in the present review. The sources of information used for the charts and summaries of the work done, are given below in the form of an annotated bibliography. Many of the publications are not regular scientific journals and it has sometimes been difficult to assign authorship to the work. The positions plotted on the charts are approximate, especially where many neighbouring observations have been made. The annotations are necessary for an understanding of the later sections of this review.

ANGOT, M. (1959). Premiers resultats obtenus par l'Institut francais d'Oceanie sur la production primaire dans le sud-ouest du Pacifique. Internat. Oceanogr. Congress, New York. 6p.

Cruise "Astrolabe" in May-June and "Boussole" in November 1958 collected samples at 0 and 25 m in the area New Caledonia, New Hebrides to San Cristobal. On "Astrolabe" samples were collected at 0800 and on "Boussole" at 0800 and 1400; the Richards-Thompson method was used on board. Non-astacin values were always negative.

ANGOT, M. (1959). Orsom III: resultats de la croisiere "Boussole." Pt. 2: Chimie, productivite et zooplancton. O.R.S.T.O.M., I.F.O., Rapp. Sc. No. 13, p. 61.

Samples were taken at 0800 and 1400 at 0 and 25 m northward from New Caledonia during November 1958. Analyses by the method of Richards-Thompson were made on board. The results are used in Figs. 1 and 2.

ANGOT, M. (1959). Orsom III: resultats de la croisiere "Astrolabe." Pt. 2: Chimie, productivite et zooplancton. O.R.S.T.O.M., I.F.O., Rapp. Sc. No. 9, p. 62.

Samples were taken at 0800 at 0 and 25 m around New Caledonia and northward during May-June 1958. Analyses by the method of Richards-Thompson were made on board. The results are used in Figs. 1 and 2.

ANGOT, M. (1960). Orsom III: resultats de la croisiere "Choiseul." Pt. 2: Chimie, productivite, phytoplancton qualitatif. O.R.S.T.O.M., I.F.O., Rapp. Sc. No. 16, p. 49.

Samples were taken in the region south-east of New Caledonia during May 1959. At 0700 samples were taken at 0, 25, and 50 m to give the mean value for the 0-50 m layer and at 50, 75, and 100 m for the 50-100 m layer. At 1400 surface samples were taken and 0, 33, 66, and 100 m samples for the 0-100 m mean value. The areas under the absorption curves were calculated and are given as "surfaces encadrees"; these are suggested as better representations of the pigment values. Results (Richards-Thompson) for chlorophyll-a, -b, and -c and astacin carotenoids are given; the results are used in Figs. 1 and 2.

ANGOT, M. (1961). Orsom III: resultats de la croisiere "Dillon." Pt. 2: Chimie et biologie. O.R.S.T.O.M., I.F.O., Rapp. Sc. No. 19, p. 50.

A critique of the Richards-Thompson method is given together with the details of the improved modification used. Samples were taken to the north-west of New Caledonia during May 1960 at 0800. Mixed 0, 25, and 50 m samples represented the 0–50 m layer, and 50, 75, and 100 m the 50–100 m layer. Filtration was done at once but some filters were not dissolved in acetone until the end of the cruise. Results are given as chlorophyll-a (results used in Fig. 1) and as "surfaces encadrees" for the euphotic zone (77-95 m) and 0-100 m layer at 15 stations. Chlorophyll-a ranged from 0.2–1.0 mg/m^3 (mean = 0.4).

C.S.I.R.O. Aust. (1958) Scientific Report of Cruise 7/58 on F.R.V. "Derwent Hunter." Div. Fish. Oceanogr. Rep. No. 27, p. 49.

Vertical profiles (0, 25, 50, and 100 m) are given for two stations off Sydney in April 1598. The results are used in Figs. 1–5.

C.S.I.R.O. Aust. (1959) Scientific Reports of a Cruise on H.M.A.S. Ships "Queen-

borough" and "Quickmatch" March 24–April 26 (1958). Div. Fish. Oceanogr. Rep. No. 24, p. 19.

Samples were usually taken at either 0500 or 1700 at 0, 25, and 50 m and analysed ashore a few weeks later by the Richards-Thompson method. Results are given as graphs for the lines Brisbane–Noumea–Auckland–Sydney. The results are used in Figs. 1–5.

C.S.I.R.O. Aust. (1960) Scientific Reports of Cruises 10-11/58 and 13-18/58 on F.R.V. "Derwent Hunter." Div. Fish. Oceanogr. Rep. No. 30, pp. 4, 10, 14, 16, 23, 31, 38, and 52.

Vertical profiles (some down to 200 m) are given for several stations off Sydney during June–November 1958. The results are used in Figs. 1–5.

C.S.I.R.O. Aust. (1960) Oceanic observations in Antarctic waters, M.V. "Magga Dan" 1959. C.S.I.R.O. Aust. Oceanogr. Sta. List 44.

Samples were taken at 0 and 25 m from the ice-edge to Australia. Analyses by the Richards-Thompson method on filters stored during the cruise gave results which were nearly always less than 1.0 mg or MSPU/m^3. The highest chlorophyll-a value was 0.44. The results are used in Figs. 1–5.

DOTY, M. S. (1956). Current Status of Carbon-fourteen Method of Assaying Productivity of the Ocean. Mimeo, University of Hawaii.

Appendix VI gives the results of Smith Cruise 31 (part of the Eastropic Expedition) in the eastern equatorial Pacific Ocean during October–December 1955. Surface samples were taken at 0800–1000. The results are used in Figs. 1–3.

DOTY, M. S. (1959). Current Status of Carbon-fourteen Method of Assaying Productivity of the Ocean. Mimeo, University of Hawaii.

Appendix II gives the details of the Richards-Thompson method used. Results are given from the Hawaiian Islands; Eastern Central Pacific and Tuamotos (Smith Cruise 38); Northern Marshalls; North Pacific (Smith Cruise 46); and Central Pacific (Gilbert Cruise 43). The results of Smith Cruise 38 (January– March 1957; surface samples at about 1200) are used in Figs. 1–3.

GRAHAM, H. W. (1943). Chlorophyll-content of marine plankton. J. Mar. Res., 5(2): 153-160.

During August 1941 and July–August 1942, 24 samples taken off La Jolla contained 0–1.9 mg/m^3 chlorophyll-a (spectrophotometric method).

HOKKAIDO UNIVERSITY (1961). Data Record of Oceanographic Observations and Exploratory Fishing. No. 5, p. 135.

Surface chlorophyll-a was estimated (Richards-Thompson method) in 71 samples on Oshoro Maru Cruise 46 to the Bering Sea and North Pacific. The results are used in Fig. 1.

HOLMES, R. W. (1958). Physical, chemical, and biological oceanographic observations obtained on Expedition Scope in the eastern tropical Pacific, November–December 1956. U. S. Fish and Wildlife Service Spec. Sci. Rep.: Fish. No. 279.

Samples were taken, some to 200 m, and analysed for chlorophyll-a (Richards-Thompson). Most of the surface ones were less than 0.5 mg/m^3 and only those at 14°17′N., 96°34′W.; 11°13′N., 90°55′W.; 7°37′N., 82°25′W., and 14°37′N., 100°09′W., were plotted in Fig. 1; these were between 0.5 and 1.0 mg/m^3. The deep ones have been used in Fig. 4.

HOLMES, R. W. (1958). Surface chlorophyll "a," surface primary production, and zooplankton volumes in the Eastern Pacific Ocean. Rapp. Cons. Explor. Mer. 144: 109-116.

Summary and discussion of results then available.

HOLMES, R. W. and BLACKBURN, M. (1960). Physical, chemical, and biological observations in the eastern tropical Pacific Ocean Scot Expedition, April-June 1958. U. S. Fish and Wildlife Service Spec. Sci. Rep.: Fish No. 345.

Vertical profiles of chlorophyll-a (Richards-Thompson) down to as far as 150 m are given. Most samples were taken at 1030. The results are used in Figs. 1 and 4.

HOLMES, R. W., SCHAEFFER, M. B., and SHIMADA, B. M. (1957). Primary production, chlorophyll, and zooplankton volumes in the tropical Eastern Pacific Ocean. Inter.-Amer. trop. Tuna Comm. Bull. 2(4): 129-169.

During October-December 1955 surface samples (a few to 100 m) were taken in the eastern Pacific as part of the Eastropic Expedition. The Richards-Thompson method was used but only for chlorophyll-a. Nearly all the results were less than 0.5 mg/m^3 and have not been plotted; they confirm for a different season those obtained by Holmes and Blackburn (1960) for almost the same area. The only results plotted in Fig. 1 are 1.06 mg/m^3 at 14°41'N., 95°42'W.; 0.5 at 1°13'S., 83°51'W.; 2.0 at 3°42'S., 83°06'W., and 0.6 at 1°59'S., 83°20'W. The few deep results are plotted in Fig. 4.

HUMPHREY, G. F. (1960). The concentration of plankton pigments in Australian waters. C.S.I.R.O. Aust. Div. Fish. Oceanogr. Tech. Pap. No. 9.

Gives a critique of sampling and analytical problems, particularly the Richards-Thompson method. Gives results for February-December 1958 of weekly samples off Sydney.

ICHIMURA, S. and SAIJO, Y. (1959). Chlorophyll content and primary production of the Kuroshio off the southern mid-coast of Japan. Bot. Mag., Tokyo, 72: 193-202.

Chlorophyll values (probably total chlorophyll because method depends on colorimetric estimation of phaeophytins) to 100 m for August 1957 and May 1958.

KING, J. E., AUSTIN, T. S., and DOTY, M. S. (1957). Preliminary report on Expedition Eastropic. U. S. Fish and Wildlife Service Spec. Sci. Rep.: Fish. No. 201.

Gives the modification of the Richards-Thompson method used on Smith Cruise 31.

McALLISTER, C. D., PARSONS, T. R., and STRICKLAND, J. D. H. (1959). Data record. Oceanic fertility and productivity measurements at Ocean Weather Station P. July and August 1959. Fish. Res. Bd. Can. MS Rept. Ser. (Oceanogr. and Limnol.) No. 55.

Values for chlorophyll-a and -c, and carotenoids were obtained by the Richards-Thompson method. Samples were taken at various depths, one at 1000 m. Results were usually less than 1 mg or MSPU/m^3.

McALLISTER, C. D., PARSONS, T. R., and STRICKLAND, J. D. H. (1960). Primary productivity and fertility at Station "P" in the north-east Pacific Ocean. J. Cons. Int. Explor. Mer. 25(3): 240-259.

Samples were taken at 0630-0700 at several depths from 0.50 m in July-August 1959.

OGURI, M. (1960). Carbon fixation and phytoplankton data from Hugh M. Smith Cruise 46. U. S. Fish and Wildlife Service Spec. Sci. Rep.: Fish. No. 358, p. 97.

During July-September 1958, surface and 20 m samples were collected, filtered and filters returned to the laboratory for analysis by the Richards-Thompson method for chlorophyll-a, -b, and -c, and carotenoids. The results are used in Figs. 1-3.

PARSONS, T. R. (1960). A data record and discussion of some observations made in 1958-60 of significance to primary productivity research. Fish. Res. Bd. Can. MS Rep. Ser. (Oceanogr. and Limnol.) No. 81.

Gives chlorophyll-a (0.17–0.95 mg/m^3), -b (0–0.25 mg/m^3), and -c (0.12–1.5 MSPU/m^3)

and plant (0–0.50 MSPU/m^3) and animal (0–1.27 MSPU/m^3) carotenoids (Richards-Thompson) for groups of samples taken between November 22, 1958 and June 29, 1960. The depths in the groups varied but some went to 100 m. The results are used in Figs. 1-5.

SAIJO, Y. and ICHIMURA, S. (1960). Primary production in the north-west Pacific Ocean. *J. Oceanogr. Soc. Japan* 16: 139-145.

Similar to Ichimura and Saijo (1959) but also gives results for July-September 1958. The values in this paper have been used in Figs. 1 and 4.

SCRIPPS INSTITUTION OF OCEANOGRAPHY (1958–1959). Scripps tuna oceanography research (STOR) program: quarterly progress reports. Nos. 7 and 9. La Jolla.

Chlorophyll-a was estimated on Cruise TO 59–1 in January-February 1959 from San Diego to Panama and 59–2 in August-September 1959 from San Diego to Tehuantepec. Results are not available.

SHIMADA, B. M. (1958). Diurnal fluctuation in photosynthetic rate and chlorophyll "a" content of phytoplankton from eastern Pacific waters. *Limnol. Oceanogr.* 3(3): 336-339.

Surface samples were taken every two hours for 46 hours on May 28-29, 1957 at Clarion Island (18°21'N., 114°44'W.). Chlorophyll-a values (Richards-Thompson) varied from 0.08 to 0.15 mg/m^3.

YENTSCH, C. S. (1956). Plant pigment determinations. Univ. Wash. Spec. Rep. No. 22, p. 103.

Chlorophyll-a content of 61 samples collected at 10 m in the north-east Pacific during NORPAC. The results (Richards-Thompson) have been used in Fig. 4.

Distribution of Pigments in the Pacific Ocean

Figure 1 shows the distribution of surface chlorophyll-a. Most of the observations were made in 1955-61 and modifications of the Richards-Thompson method were used. For comparison, the results of Saijo and Ichimura (1960) have been included although these are probably total chlorophyll. Large class intervals were used in the figure because samples were taken during different seasons and at different times of day. Further, there is not sufficient biological or chemical environmental description for proper discussion of finer differences. The Australian results are not shown individually because, with the exception of 27 in the rectangle 150-160°E., 30-40°S., equivalent to 1, all were less than 0.5 mg/m^3. The area of the Australian investigations is shown in the figure; about 250 surface estimations were made, those more than 100 miles from Sydney being in the period January-April. The French results are not shown individually because so many were obtained in overlapping areas. Probably only the values for Cruise "Dillon" should be used; on earlier cruises the analytical method was not completely developed.

For none of the oceanic areas investigated is there sufficient information to give any idea of seasonal variation. The only part of the Pacific Ocean for which there is such information is that within ten miles of Sydney. There, two stations have been sampled almost weekly from February 1958 to December 1960 during which period the surface chlorophyll-a has varied from 0.1–7.3 mg/m^3. Such wide variations cannot be expected in the open ocean. The following discussions on differences in productivity as measured by chlorophyll-a are only tentative.

Bearing in mind the limitations referred to above, the information shows that the north-east Pacific was richer than the equatorial and the south-western areas. For example, the mean value on "Smith" Cruise 46 from Hawaii to the north was 0.6 mg/m^3 whereas the corresponding value for "Smith" Cruise 31 as part of the Eastropic investigations from the central Pacific to Mexico and for Cruise "Dillon" to the north-west of New Caledonia were each 0.4 mg/m^3.

Figure 2 shows the distribution of surface chlorophyll-b. The 250 estimations in the Australian area were each less than 0.5 mg/m^3. The results for the French area were obtained

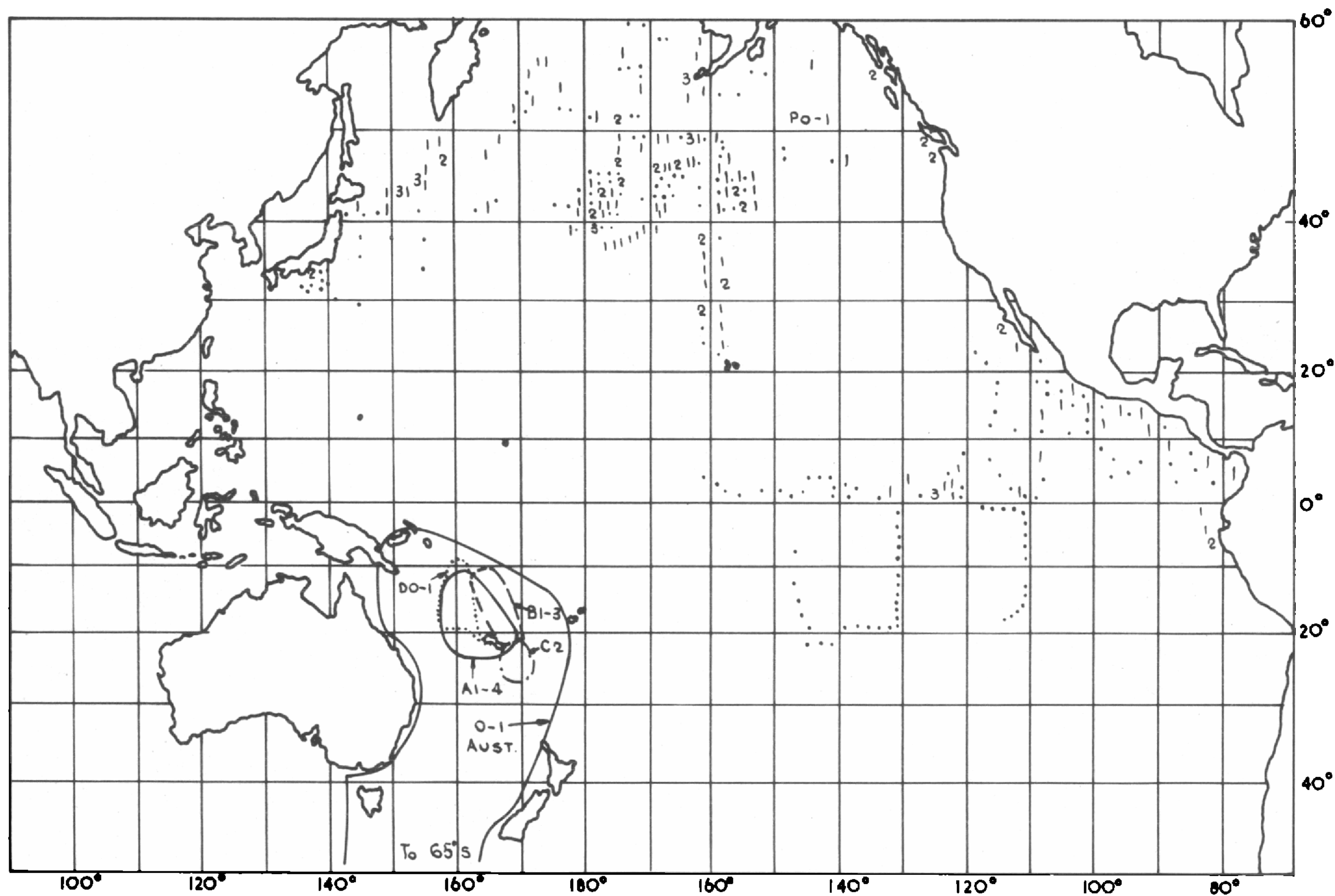

Figure 1 — Distribution of chlorophyll-a at 0 m.: . = 0–0.49 mg/m^3; 1 = 0.5–1.49 mg/m^3; 2 etc. = 1.5–2.49 etc. mg/m^3; A, B, C, D = areas covered by "Astrolabe," "Boussole," "Choiseul," "Dillon"; Aust. = area covered by Australian cruises; P = position of Station P (Parsons 1960).

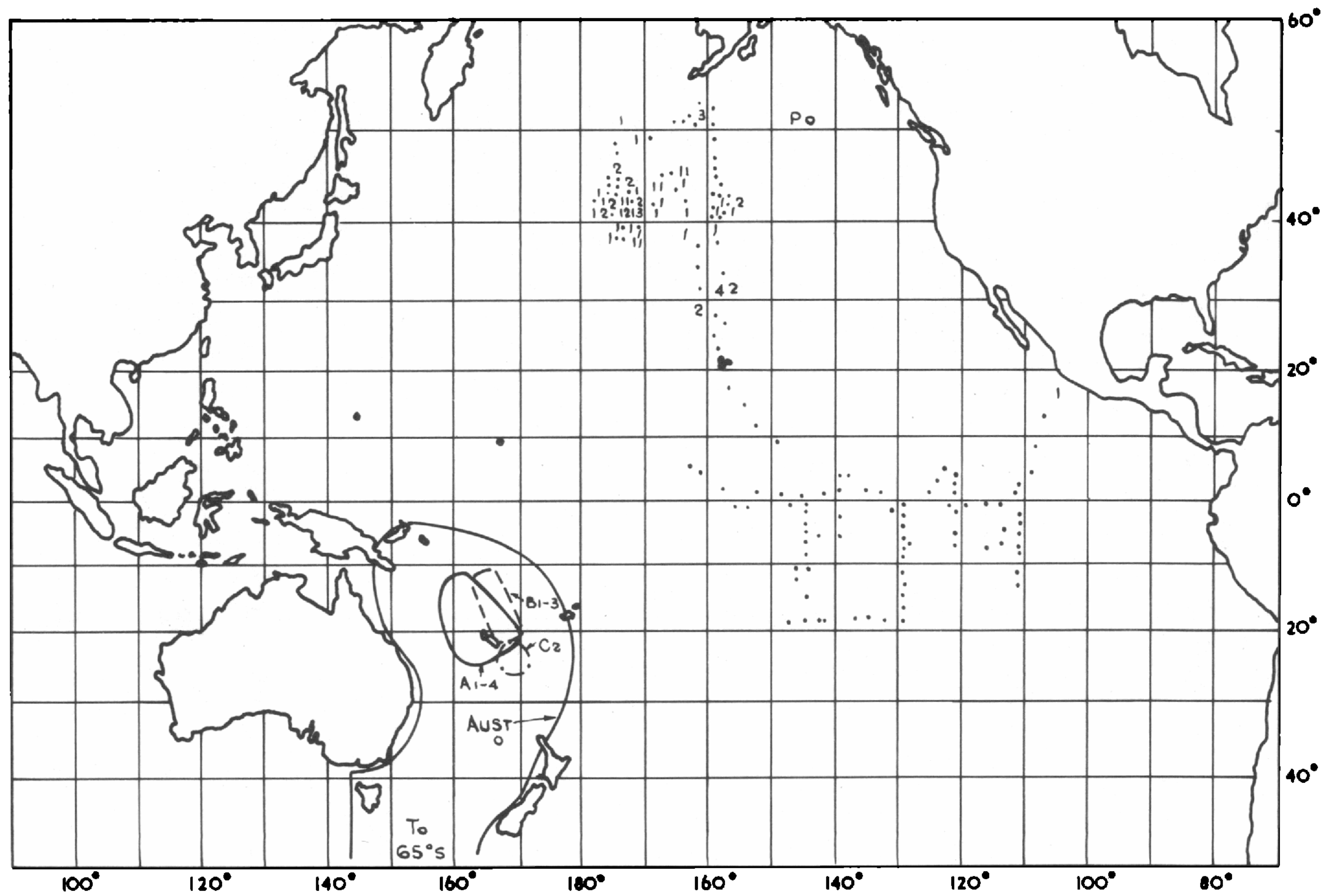

Figure 2—Distribution of chlorophyll-b at 0 m. Symbols as for Figure 1.

before the analytical method was improved and are probably too high. The results from the seasonal study off Sydney were between 0 and 0.52 mg/m^3. It seems that, as with chlorophyll-a, the northern Pacific was richer than the equatorial and the south-western areas.

Figure 3 shows the distribution of surface chlorophyll-c. The French areas are not shown, the results being 4-26 for "Astrolabe," 7-23 for "Boussole," and 12-25 for "Choiseul." Chlorophyll-c results are not available for "Dillon," the cruise for which an improved modification of the Richards-Thompson method was used. The Australian results north of 46°S. are plotted (only one third of the observations taken in the rectangle 150-160°E., 30-40°S. are used). It can be seen that the northern Pacific was the richest area. Of the area covered by the Australian investigations the rectangle near Sydney was the richest; during the same period the values at the station near Sydney varied from 0–6.11 mg/m^3. Of the three pigments discussed so far, it is chlorophyll-c which was present in greatest concentration at the surface.

Figure 4 shows the distribution of chlorophyll-a between 1 and 25 m. (Only one third of the observations taken in the rectangle 150-160°E., 30-40°S. are used). The northern Pacific was again the richest area. In the eastern and south-western areas this layer (samples were usually at 25 m) was richer than the surface. The results available for other depths (but not plotted here) show that the layer around 50 m was as rich as the surface for these two areas but at 75 and 100 m, less than 10 per cent of the samples had more than 0.5 mg/m^3 chlorophyll-a. In the heavily sampled Australian rectangle about 90 samples were taken at each depth; the numbers of samples with concentrations greater than 0.5 mg/m^3 were: 27 at 0 m, 39 at 25 m, 30 at 60 m, and 5 at 75 or 100 m. It follows that surface samples are insufficient when assessing the chlorophyll-a content of an area or when comparing areas.

The northern Pacific was the only area where chlorophyll-b occurred to a significant extent below the surface. The values at 25 m were a little or less than those at the surface.

Comparisons of chlorophyll-c content below the surface can be made only between the Australian area and the central north Pacific. Figure 5 shows that the northern area was the richer of the two; the 1-25 m layer was richer than the surface. The values for the Australian area (only one third of the observations taken in the rectangle 150°-160°E., 30-40°S. are used) include some at depths to 150 m; the concentration of -c did not decrease until 100 m. The maximum concentration of -c usually occurred below the surface; only 10 per cent of the Australian stations showed a surface maximum.

It seems from the above description of the variation in chlorophyll concentrations between the northern, equatorial and south-western areas of the Pacific, that concentration increases with latitude. Such a conclusion is supported by Table 2 which shows the mean concentration of chlorophylls in the various parts of the Australian area during the summers of 1958-61.

Analytical Methods

In 1930, Kreps and Verjbinskaya gave values of 0–0.82 mg/m^3 for chlorophyll in the Barents Sea. Their method was to make a photoplankton collection with a net and suspend the phytoplankton in 1 litre of sea-water; 25 ml were centrifuged, the residue treated with 4 ml alcohol and the chlorophyll estimated spectrophotometrically. No other details were given. This basic method has passed through the many stages of simplification and refinement and now the Richards-Thompson (1952) method (usually with slight modifications to suit the actual working conditions) is the one most used. Table 3 shows some details of the various methods which have been used in the Pacific Ocean.

The following comments are made on this Table.

1. The Richards-Thompson method needs only a few litres of water (compared to the 10 to 60 litres used by Ichimura and Saijo).

2. Most workers use $MgCO_3$ in order to prevent phaeophytin formation although none has proved phaeophytin is formed without it. $MgCO_3$ may increase the speed of filtration; it may help pigment extraction if the acetone suspension is ground with a glass rod in the centrifuge tube; it may give cleaner centrifugation; and it may diminish loss of plankton by acting as a filler when transferring the filter from a storage, to an extraction tube. If an aqueous suspension of $MgCO_3$ is added after the plankton are on the filter (Doty, 1959a), filtration should be rapid so that no cytolysis occurs.

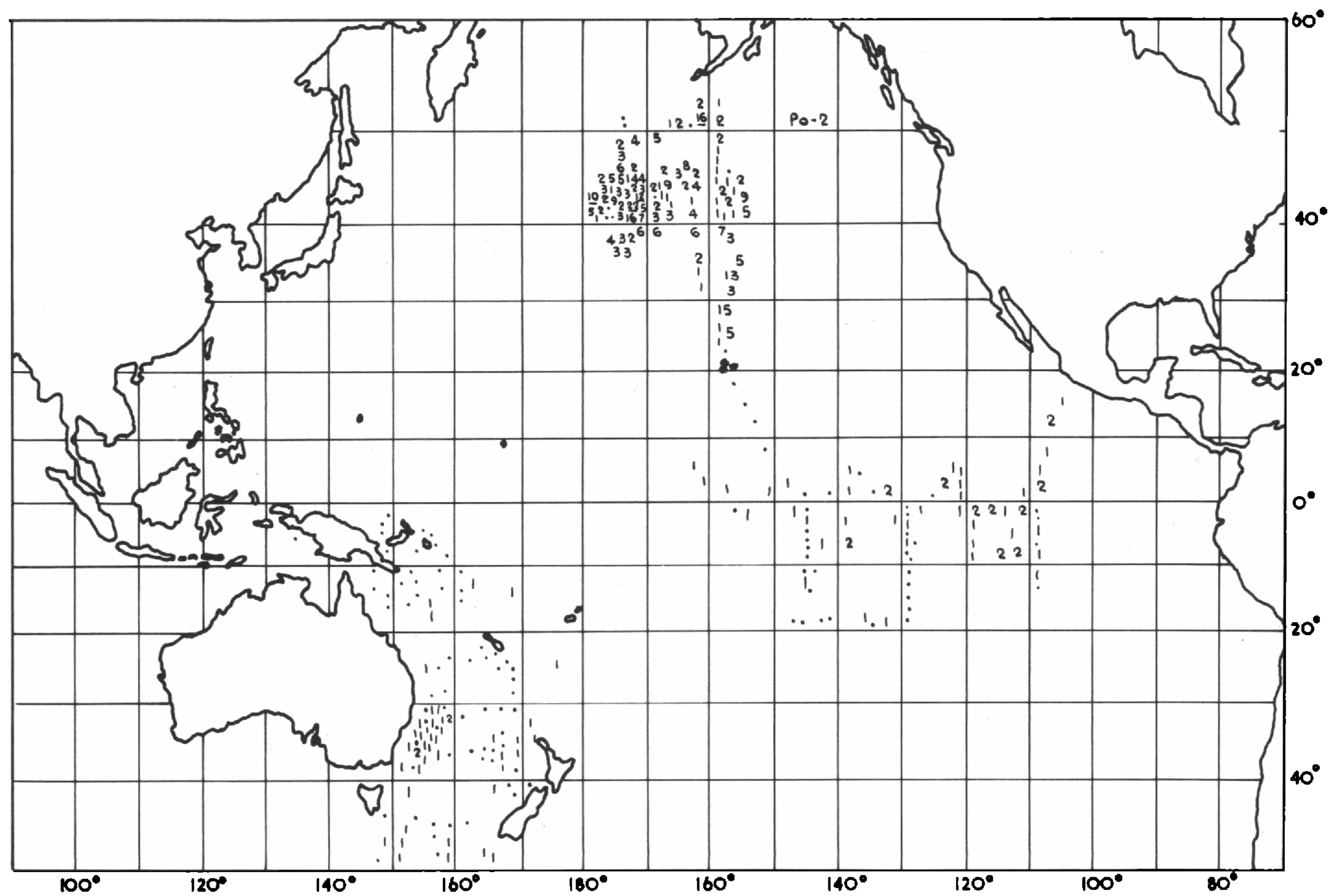

Figure 3—Distribution of chlorophyll-c at 0 m. Symbols as for Figure 1.

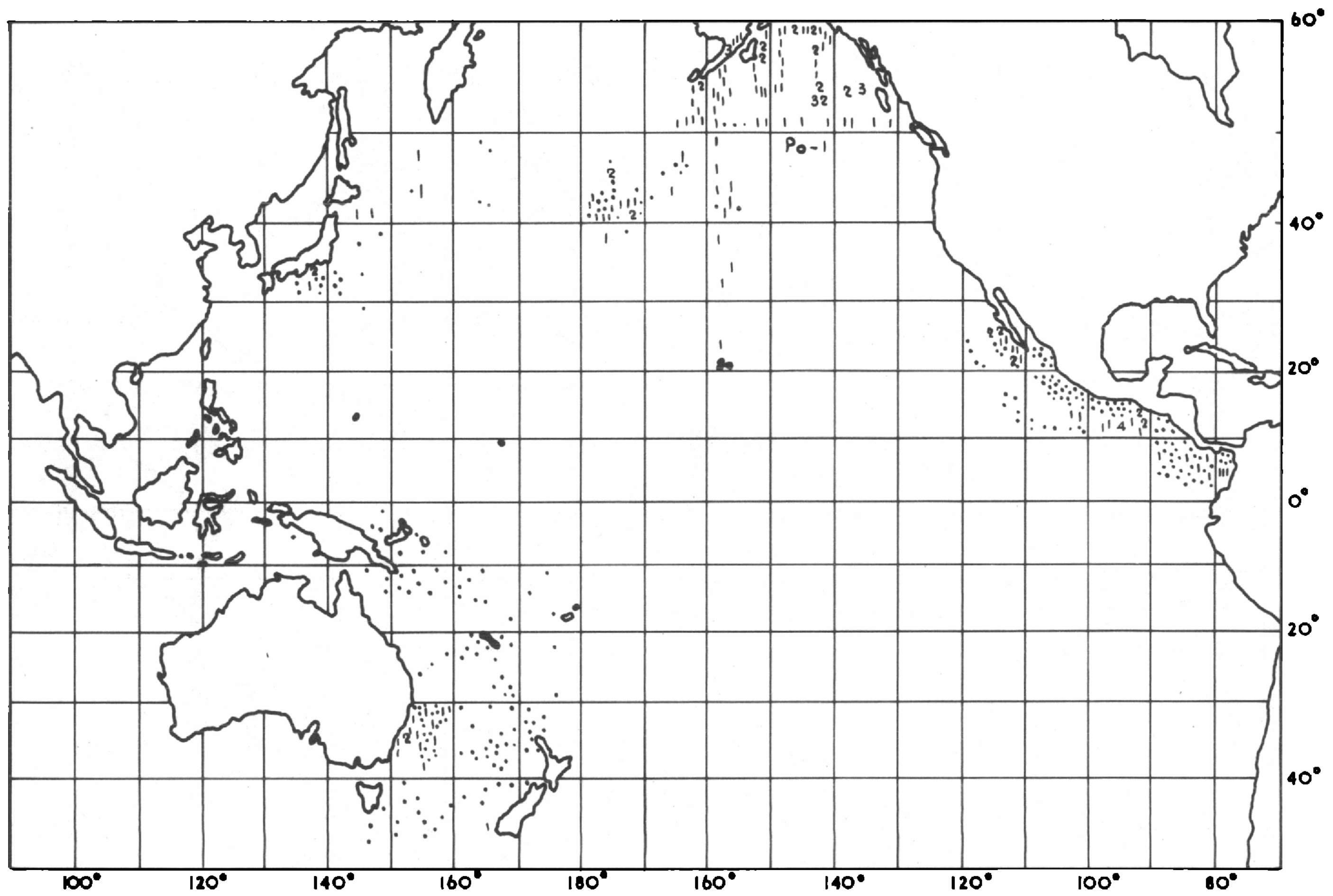

Figure 4—Distribution of chlorophyll-a at 1–25 m. Symbols as for Figure 1.

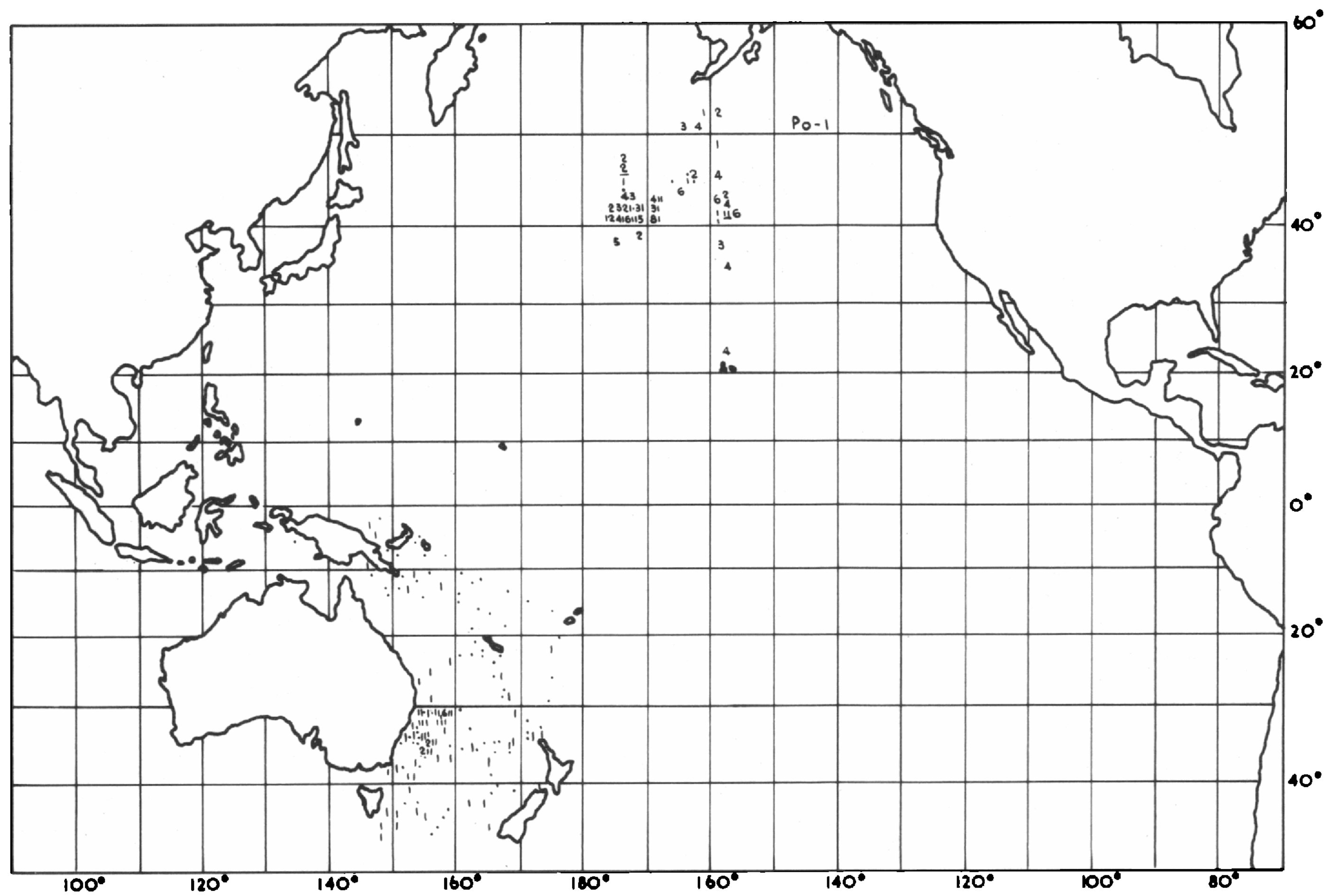

Figure 5—Distribution of chlorophyll-c at 1–25 m. Symbols as for Figure 1.

Table 1—Algal Pigments

	Chloro-phyceae	Eugleno-phyceae	Phaeo-phyceae	Bacillario-phyceae	Chryso-phyceae	Xantho-phyceae	Dino-phyceae	Rhodo-phyceae	Myxo-phyceae
Chlorophylls:									
Chlorophyll-a	+++	+++	+++	+++	+++	+++	+++	+++	+++
Chlorophyll-b	++	+	–	–	–	–	–	–	–
Chlorophyll-c	–	–	+	+	+	–	+	–	–
Chlorophyll-d	–	–	–	–	X	–	–	+	–
Chlorophyll-e	–	–	–	–	X	+	–	–	–
Carotenes:									
α-Carotene	+	X	–	–	X	X	–	+–	X
β-Carotene	+++	+++	+++	+++	+++	+++	+++	+++	+++
ϵ-Carotene	–	X	–	+	X	X	X	X	X
Flavacin	–	X	–	–	X	X	X	X	+
Xanthophylls:									
Lutein	+++	?	–	–	+	–	–	++	?
Zeaxanthin	+	X	–	–	–	–	–	X	?
Violaxanthin	+	X	+	–	–	X	–	X	X
Flavoxanthin	?	X	+	–	–	X	X	X –	X
Neoxanthin	+	X	+	–	–	–	–	X	X
Fucoxanthin	–	–	++	++	+	–	–	?	X
Neofuco-xanthin A	–	–	+	+	+	–	–	X	X
Neofuco-xanthin B	–	–	+	+	+	–	–	X	X
Diatoxanthin	–	–	?	+	+	–	–	X	X
Diadinoxanthin	–	–	?	+	+	–	+	X	X
Dinoxanthin	–	–	?	–	+	–	+	X	X
Neodinoxanthin	–	–	–	–	–	–	+	X	X
Peridinin	–	–	–	–	–	–	++	X –	X
Myxoxanthin	–	–	–	–	–	–	–	X	++
Myxoxantho-phyll	–	–	–	–	–	–	–	X	++
Unnamed	X	+	+	X	–	++	X	?	?
Phycobilins:									
r-Phyco-erythrin	–	–	–	–	–	–	–	+++	–
r-Phyco cyanin	–	–	–	–	–	–	–	+	–
c-Phyco-erythrin	–	–	–	–	–	–	–	–	+
c-Phyco-cyanin	–	–	–	–	–	–	–	–	+++

+++ indicates the principal pigment of the group.
++ indicates a pigment comprising less than half of the total pigments of the group.
+ indicates a pigment comprising a small fraction of the total pigments of the group.
– indicates absence of the pigment.
X indicates incomplete examination, especially of minor constituents.
? indicates small quantities of pigment whose source or identification is uncertain.

Table 2—Regional Concentration of Chlorophylls in S.W. Pacific Ocean

The figures are mean values (Richards-Thompson units) for a particular depth, or integrated for the water column.

	Tropical 0–20°S	N. Tasman 20–35°S	Central Tasman 35–40°S	S. Tasman 40–50°S
Chlorophyll-a				
0 m	0.06	0.06	0.11	0.16
25	06	07	10	17
50	08	09	13	19
75	–	–	25	16
100	13	11	22	09
150	06	–	09	08
0–100	09	09	14	15
Chlorophyll-b				
0 m	0.04	0.05	0.06	0.09
25	05	06	06	09
50	05	07	07	09
75	–	–	13	08
100	08	08	09	07
150	05	–	06	06
0–100	06	07	07	09
Chlorophyll-c				
0 m	0.30	0.35	0.41	0.47
25	31	39	47	50
50	30	41	50	58
75	–	–	–	58
100	49	54	54	42
150	27	–	45	48
0–100	35	43	49	51

Table 3 — Details of Analytical Methods

	Richards-Thompson	Creitz-Richards	Astrolabe	Boussole	Angot		Doty	
					Choiseul	Dillon	Smith 31	Smith 38 and 46
Volume, 1	1–2		4		2	2–4	4–5	1–4
$MgCO_3$	+	+			–	–	+	Aq. suspn. after filtrn.
Filter	Foerst centrifuge & wash with water	AA	HA			HA	AA	HA
Dry	vac. des.	vac. des.	no		no		des.	des.
Storage		up to 3 wk in cold	none		none	des.	dark	cold
Acetone	5 ml 90%		20 ml 90%		10 ml 90%	10 ml 90%	10 ml 90%	5 ml 90%
Extraction	dark 18–24 hr				dark $^3/_4$ hr at least	24 hr	cold 18–24 hr	cold 18–24 hr
Centrifuge	3 min clinical		none	1 min 500 g	60 sec at least; 500 g	30 min 3,000 r	5 min 3–4,000 r	5 min 3–4,000 r
Re-extract							1–2 ml	
Cell	1 cm		10 cm		1 cm			5 cm
Turbidity		750			750		750	
Remarks			non-astacin always negative				read at 665, 645, 630, 550	

Table 3—Continued

	Graham	Hokkaido University	Holmes-Blackburn; Holmes	Holmes, Schaefer & Shimada	Humphrey	Ichimura-Saijo	McAllister, Parsons & Strickland	Shimada	Yentsch
Volume, l	4	2–11	3–6	4–8	4–5	10–60		6	1.5–3
$MgCO_3$	–	–	+	+	+	–		+	
Filter	Fine chemical paper & sintered filter	0.6 μ pores	HA	HA	HA	4 sheets Toyo 101- steam 1 min	AA		AA
Dry		boiling water, then dried	vac. des.		vac. des.	air			yes
Storage		dark, cold			up to 4 wk	des.			
Acetone	10 ml 80%	5 ml 90%	3 ml 90%	3 ml 90%	5 ml 90%	10 ml 80%		3 ml 90%	
Extraction			dark, 10°C	dark, cold	dark	dark		10°C	
	1 hr	18 hr	10–12 hr	10 hr	21 hr	24 hr		12 hr	
Centrifuge	sintered filter			+	10 min 4300/g			4,500 r	
Re-extract			1–2 ml	3 ml	if residue colored			3 ml	
Cell		1 cm	10 cm	10 cm	1 cm		10 cm	10 cm	1 cm
Turbidity			750		750		750	750	
Remarks	read at 668				subtract 750 value if above 0.005	extracts pheophytins from acetone by benzene- uses a red filter in photoelectric colorimeter	unspecified turbidity factor		

3. As a general procedure, a filter is preferable to a centrifuge because under certain conditions the latter may not retain all the plankton (Creitz and Richards, 1955). Washing the centrifuged plankton with water (Richards with Thompson, 1952) should be avoided because of the danger of cytolysis.

4. Most workers store their filters rather than analyze on board. More justification of this procedure is needed.

5. A reading at 750 mμ is usually made as a check on turbidity but exact details are needed on how this reading is used when computing results.

6. Richards with Thompson (1952) note that small negative values within the instrumental error are frequently found for chlorophyll-b. Other workers (Angot, 1959b; Doty, 1959a; Humphrey, 1960) have found larger negative values for non-astacin pigments and occasionally for chlorophyll-b and astacin pigments McAllister, et al., (1959) give the following values for precision: chlorophyll-a ± 0.06 mg m^3; chlorophyll-c, plant carotenoids and animal carotenoids ± 0.05 $MSPU/m^3$.

The rapidity and convenience of the Richards-Thompson method have enabled a large number of determinations to be made of pigments which previously could not be estimated with such simplicity. Only a few workers have used the full range of the method and obtained information on all the pigments. Others have determined only chlorophyll-a. This could show a lack of interest in the other pigments but in general there is a feeling that the method is not reliable when used for pigments other than chlorophyll-a. This lack of reliability is shown not only by the negative values but also by the fact that the ratios of chlorophylls-c and -b to -a found for sea-water samples are much greater than those for algal cultures by other methods (Table 4). The cultures used by Jeffrey (1961) were 2-4 weeks old and were grown at 400 foot-candles at 18°C; pigments were separated by paper chromatography, eluted and measured individually using the spectral constants given by Smith and Benitez (1955).

Table 4—The Ratios of Chlorophylls-b and -c to -a for Sea-water Samples and Algal Cultures

	mg b/mg a	MSPU c/mg a
ANGOT		
"Astrolabe," range	0.8–0.9	4.4–6.5
"Astrolabe," mean	0.8	5.8
DOTY		
"Smith 31," range	0–1.7	0.1–9.0
"Smith 31," mean	0.5	3.6
HUMPHREY		
"Gascoyne $^1/_{60}$," range	0–1.0	1.3–12.3
"Gascoyne $^1/_{60}$," mean	0.7	5.7
OGURI		
"Smith 46," range	0–1.9	0–14.7
"Smith 46," mean	0.8	4.5
PARSONS		
"Station P," range	0–0.9	0.3–3.0
"Station P," mean	0.1	1.2
JEFFREY (1961)*		
Dunaliella terteolecta	0.4	
Nannochloris atomus	0.5	
Phaeodactylum tricornutum		0.4
Skeletonema costatum		0.9
Nitzschia closterium		0.6
Isochrysis galbana		0.7
Sphaleromantis sp.		0.5
Gymnodinium sp.		1.0

*Recalculated by Richards-Thompson absorption coefficients.

In discussing over-all errors in the method, Richards with Thompson (1952) give 43% for chlorophyll-c when measuring concentrations about 0.75 MSPU/L of acetone extract and 14% for chlorophyll-a at a concentration about 1.0 mg/L. Even allowing for errors of these magnitudes, there is a big difference between the sea-water and culture values given in Table IV. At low concentrations of pigments (especially when using 1 cm cells), small errors of reading the spectrophotometer sometimes make big differences in the results and thus contribute to the wide ranges of the ratios found for sea-water samples.

Table 5 — Effects of Errors of Reading Optical Densities

	Observed		Error at 665 mμ 0.001 (0.002)		Error at 645 mμ 0.001 (0.002)		Error at 630 mμ 0.001 (0.002)	
Wave Length	Optical Density	Concentration*	Optical Density	Concentration*	Optical Density	Concentration*	Optical Density	Concentration*
665 mμ	00.037	0.054	0.036 (0.035)	0.53 (0.51)	–	– (0.55)	–	– (–)
645	0.012	0.01	–	– (0.02)	0.011 (0.010)	–0.02 (–0.04)	–	0.02 (0.03)
630	0.013	0.61	–	0.62 (0.64)	–	0.64 (0.67)	0.012 (0.011)	0.50 (0.39)
	b/a	0.02	–	0.02 (0.04)	–	0 (0)	–	0.04 (0.06)
	c/a	1.1	–	1.2 (1.3)	–	1.2 (1.2)	–	0.9 (0.7)

– = value unchanged from original.
* concentrations are given in the order chlorophyll-a, -b, and -c in Richards-Thompson units.

Table 5 shows the effect of changes of 0.001 and 0.002 (errors easily made) in the optical densities at 665, 645, and 630 mμ found using 1 cm cells. The values used, and the concentrations of pigments found are typical of many oceanic samples. It should be noted that chlorophyll-a values are not significantly affected by changes at other than its own peak (665 mμ). The change in the reading at 645 mμ made the chlorophyll-b value slightly negative; this shows that the small negative values often found are not to be interpreted as indicating that there is something fundamentally wrong with the Richards-Thompson method. This change at 645 mμ also increased the chlorophyll-c value slightly and brought the ratio of c/a from 1.1 to 1.2. When the reading at 630 mμ was changed, the chlorophyll c value decreased, the ratio c/a falling as low as 0.7. Therefore in some cases values of c/a greater than 1 may be artefacts due to instrumental errors; however this explanation would not be sufficient in cases where c/a is large. To get a large effect on c/a, large errors would need to be made in the readings (Table 6). Errors in reading are more effective the lower the reading and therefore wide cells are preferable. Nevertheless, large values of c/a were found by Doty (1956), Oguri (1960) and Parsons (1960) although 5 and 10 cm cells were used.

Table 6 — Changes in Optical Density Needed to Reduce Ratio of c/a to 1 and 0.5

Concentrations are given in the order chlorophyll-a, -b, -c, astacin and non-astacin in Richards-Thompson units. Optical densities (1 cm cells) are in the order 665, 645, 630, 510, and 480 mμ.

Sample where c/a = 9.0					
Observed optical density	0.010	0.010	0.014	0.020	0.035
Concentration	0.13	0.07	1.16	0.10	0.02
Optical density for c/a = 1.0			0.005		
= 0.5			0.004		
Sample where c/a = 1.5					
Observed optical density	0.020	0.010	0.009	0.013	0.025
Concentration	0.28	0.07	0.44	0.06	0.03
Optical density for c/a = 1.0			0.008		
= 0.5			0.006		
Sample where c/a = 1.2					
Observed optical density	0.041	0.013	0.015	0.024	0.056
Concentration	0.49	0	0.61	0.07	0.12
Optical density for c/a = 1.0			0.014		
= 0.5			0.011		

Difficulties also arise from the fact that the quantitative spectral characteristics of chlorophyll-c are not well known. In the Richards-Thompson method, an optical density of 10.4 is taken for chlorophyll-c at 630 mμ in a 1 cm cell containing one Specified Pigment Unit in one litre of 90% acetone. This SPU is thought to be about 1 gm. If the chlorophyll-c used by Richards and Thompson were pure, 10.4 would be its specific absorption coefficient. However, pure chlorophyll-c is still not available. Smith and Benitez (1955) suggested a value of 22.0 (ether at 628 mμ) which they calculated from magnesium determinations by assuming a molecular weight of 893, i.e., a phytyl-containing structure similar to chlorophyll-a and -b. It is probable that chlorophyll-c has no phytyl group (Smith and Benitez, 1955) and, without this, its molecular weight would be 597, giving a coefficient of 33.0.

The Richards-Thompson equations are

$$D_{665} = 0.0667\ C_a + 0.0065\ C_b + 0.0011\ C_c$$

$$D_{645} = 0.0164\ C_a + 0.0456\ C_b + 0.0044\ C_c$$

$$D_{630} = 0.0119\ C_a + 0.0127\ C_b + 0.0104\ C_c$$

where D = observed optical density.
C = concentration of pigment in the 90% acetone extract.

If 22.0 is the specific absorption coefficient of chlorophyll-c and if the shape of the absorption curve is that given by Richards (1952) the equations have different factors for C_c, i.e., 0.0023, 0.0093, and 0.0220. With a coefficient of 33.0, the factors are 0.0035, 0.0140, and 0.0330. The effects of changing to these factors are shown in Table 7. The values of chlorophyll-a and -b are independent of these changes; the greater the ratio of the optical density at 630 mμ to those at 665 and 645 mμ, the greater the change in chlorophyll-c. The coefficients 22 and 33 reduce the -c values to about a half and a third. The ratios of c/a change similarly but not sufficiently to reduce the value always to below 1.

Table 7 — Effects of Using Different Spectral Constants for Chlorophyll-c — Indicates No Change in Value; Concentrations are mg/m^3

Specific Absorption Coefficients	10.4 (Richards-Thompson)	22.0 (Smith Benitez)	33.0 (Smith Benitez) recalculated	10.4 (with 645/630 mμ = 0.22)
Chlorophyll-a	0.33	–	–	–
-b	0.20	–	–	0.22
-c	0.33	0.20	0.10	0.31
b/a	0.6	–	–	0.7
c/a	1.0	0.6	0.3	0.9
Chlorophyll-a	0.13	–	–	0.12
-b	0.10	–	–	0.15
-c	0.79	0.41	0.25	0.73
b/a	0.8	–	–	1.3
c/a	6.1	3.2	1.9	6.1
Chlorophyll-a	0.46	–	–	0.45
-b	0.17	–	–	0.24
-c	1.08	0.59	0.34	1.01
b/a	0.4	–	–	0.5
c/a	2.4	1.3	0.7	2.2
Chlorophyll-a	0.71	–	–	0.76
-b	0.08	–	–	0.12
-c	0.51	0.34	0.17	0.52
b/a	0.1	–	–	0.2
c/a	0.7	0.5	0.2	0.7

If the relative heights of the peaks at 665, 645, and 630 mμ of pure chlorophyll-c are different from those used in the Richards-Thompson equations then the values for chlorophyll-a and -b will also need recalculation. Richards with Thompson (1952) found that in 90% acetone the ratios of the optical densities were 0.11 (665/630 mμ) and 0.42 (645/630 mμ). In purification studies using column and paper chromatography, Jeffrey (unpublished) found that in 100% acetone the ratios progressed from 0.002 and 0.18 to 0.11 and 0.22 as purification proceeded. If 0.22 is the correct value of the ratio 645/630 mμ the chlorophyll-c factor in the D645 equation should be altered to 0.0023, the specific absorption coefficient at 630 mμ still being 10.4.

Changing this factor from 0.0044 to 0.0023 affects the solutions of the equations for chlorophyll-a, -b, and -c. The solutions change from

$$C_a = 15.6\ D_{664} - 2.0\ D_{645} - 0.8\ D_{630}$$

$$C_b = -4.4\ D_{665} + 25.4\ D_{645} - 10.3\ D_{630}$$

$$C_c = -12.5\ D_{665} - 28.7\ D_{645} + 109\ D_{630}$$

to

$$C_a = 15.6\ D_{665} - 1.8\ D_{645} - 1.3\ D_{630}$$

$$C_b = -5.4\ D_{665} + 23.4\ D_{645} - 2.7\ D_{630}$$

$$C_c = -11.4\ D_{665} - 26.4\ D_{645} + 101\ D_{630}$$

The effects of using these new solutions are shown in Table VII. It can be seen that chlorophyll-a and -c are almost unaffected, and -b is increased by as much as 50%. A comparison of the new solution for -b with the original Richards-Thompson solution shows that -b has become more independent of -c and it is this which is mainly responsible for the changes in the values of -b. Where the increase in -b is coupled with a low value for -a, the ratio b/a changes greatly. Elsewhere the ratios b/a and c/a are almost unaffected. Therefore again, values for c/a cannot be always reduced to those found in culture.

Another possible explanation for the high values for the ratio c/a in sea-water samples is that chlorophyll-a decomposes more readily than -c. A preliminary experiment with a bacterized culture of Gymnodinium which was analyzed weekly for 7 weeks did not confirm this possibility; the ratio c/a varied from 0.9 to 1.0 independently of the age of culture (Humphrey, unpublished).

Further evidence against chlorophyll-c having a greater resistance to decomposition than -a is provided by the results obtained by Jeffrey (unpublished) on mud samples taken at different depths off Sydney. The pigments were separated chromatographically and the amounts judged from the size and color of the sports. There was no definite evidence (Table 8) that chlorophyll-c occurred further from the shore than -a or that phaeophytin-c was less abundant than phaeophytin-a.

A practical test of the Richards-Thompson equations is to use them on known mixtures of chlorophyll-a, -b, and -c. For this, -a and -b were bought from Sandoz Ltd., Switzerland, and -c was obtained from Sargussum by solvent extraction and column chromatography. Each of these compounds was free from the other two (tested by paper chromatography). The results in Table 9 show that under the conditions used

1. where the mixture contained no chlorophyll-c, significant quantities were recorded.
2. where chlorophyll-c was present, much more than the amount added was recovered.
3. the values found for b/a were much less than the correct ones.
4. the values found for c/a were much higher than the correct ones (insufficient however, to explain the very large values found in the sea).
5. when the Richards-Thompson equations were modified to allow for a chlorophyll-c spectrum in which 645/630 mμ = 0.22, insignificant changes were observed in the results for mixtures of -a and -b. With mixtures of -a, -b, and -c, slightly better recoveries were obtained for -a, much better (up to 10%) for -c and considerably better (Table IX) for -b.

Table 8—Pigments in Mud

0 = absent, 1 = trace, 2 = definite, 3 = present, 4 = abundant

	Water depth at collecting point					
	Tidal	4 m	25 m	50 m	100 m	200 m
Chlorophyll-a	4	4	4	1	1	0
Chlorophyll-b	0	0	0	0	0	0
Chlorophyll-c	4	4	3	1	1	1
Phaeophytin-a	0	1	0	2	2	1
Phaeophytin-c	0	0	0	2	2	2
Chlorophyllide-a	0	0	0	3	1	1
Carotenes	3	3	3	3	4	3
Astaxanthin	0	0	0	3	2	3
Fucoxanthin	4	4	4	0	0	3
Remarks	diatoms present	flagellates present	some diatoms	few intact diatoms or flagellates—much decomposing material		

Table 9—Analysis of Known Mixtures of Chlorophylls

The Richards-Thompson equations were used; the modification noted is that of making 645/630 mμ = 0.22. Recoveries in solutions of chlorophyll-a or -b are calculated on the amount weighed out; recoveries in mixtures are calculated from the amounts found in single solutions by the Richards-Thompson equations. Amounts are in Richards-Thompson units. Figures in brackets are percentage recoveries.

	Recovered				
Added	Chlorophyll-a	Chlorophyll-b	Chlorophyll-c	Astacin	Non-astacin
Chlorophyll-a, 1.96	1.62	−0.07	0.14	0.01	−0.08
Chlorophyll-b, 1.20	0.15	0.94	0.11	0.08	−0.05
Chlorophyll-c, unknown	0	0	4.78	0	0.06
0.54-a + 0.63-b	0.62 (115)	0.53 (84)	0.18	0.02	0.03
1.09-a + 0.31-b	1.18 (108)	0.12 (39)	0.22	0	0.03
0.81-a + 0.47-b	0.85 (105)	0.40 (85)	0.35	0.01	0.04
1.22-a + 0.23-b	1.22 (100)	0.14 (61)	0.34	0	0.02
1.48-a + 0.09-b	1.43 (97)	−0.02 (0)	0.29	0	0.01
0.41-a + 0.47-b + 1.20-c	0.48 (117)	0.38 (81)	1.57 (131)	0.03	0
(modified equations)	0.47	0.48 (101)	1.47		
0.54-a + 0.31-b + 1.60-c	0.56 (104)	0.27 (87)	1.90 (119)	0.02	0
(modified equations)	0.55	0.40 (129)	1.77		
0.98-a + 0.19-b + 0.96-c	0.95 (97)	0.13 (68)	1.42 (148)	0.02	0
(modified equations)	0.94	0.22 (115)	1.34		
0.81-a + 0.24-b + 1.20-c	0.80 (99)	0.13 (54)	1.61 (134)	0	0.01
(modified equations)	0.80	0.23 (96)	1.50		
1.35-a + 0.08-b + 0.40-c	1.29 (96)	0 (0)	0.62 (155)	0	0.01
(modified equations)	1.29	0.03 (38)	0.60		

In view of the above discussions, it is suggested that the limitations of the Richards-Thompson method be clearly kept in mind so that users do not expect more of the method than the original authors intended. It seems that although the method can give good results for the concentrations of chlorophyll-a which are encountered in sea-water, results are only semi-quantitative for -b and the position as regards -c is obscure.

A further difficulty, and one which is common to all spectrophotometric methods, is that substances (other than those corrected for in the equations) which absorb at the wave-lengths used are counted as chlorophylls or carotenoids. These substances can be artefacts produced by methods of handling the water sample (exposure to light, cytolysis or decomposition) or naturally-occurring compounds (phaeophytins). Phaeophytin-a and -c (but not -b) have been observed in old cultures and in normally-handled sea-water samples (Jeffrey 1961). In samples taken during diatom blooms, chlorophyllides have been detected; these compounds are formed when Phaeodactylum, Skeletonema or Sphaleromantis cells are treated with water (Jeffrey, unpublished). It is probable that the presence of these compounds invalidates the Richards-Thompson equations. Not only do these considerations introduce technical difficulties into the use of the Richards-Thompson method but also they invalidate the use of any chlorophyll value obtained by the Richards-Thompson method as a measure of photosynthetic potential irrespective of what spectrophotometric constants are used.

It seems that the simplest way of estimating chlorophyll-a is to separate it (by chromatography) before spectrophotometric estimation. Such a chromatographic method has been used by Jeffrey (unpublished) on cultures, sea-water, and mud; this method has not yet been compared with the Richards-Thompson method. Another difficulty, and one which is not overcome by a preliminary separation, is that undegraded chlorophyll-a in dead or dying cells is included in chemical estimations.

Suggestions for further work

1. Complete the areal and seasonal coverages of the Pacific Ocean. Samples should be taken at 0800, because most of the samples already examined have been collected then. Some stations should be sampled at 2-hourly intervals for 48 hours. Counts of total phytoplankton and dominant species should be made; concentration of nutrient salts and light intensities should be determined. Some depth profiles to 500 m should be obtained. The Richards-Thompson method should be used, taking measurements at all the recommended wave-lengths with 5 or 10 cm cells and using the minimal quantity of acetone.

2. The various modifications of the Richards-Thompson method used should be intercalibrated. The effect of filter storage should be examined further.

3. Pure chlorophyll-c should be prepared and the Richards-Thompson method checked on a wide-range of mixtures of chlorophylls-a, -b, and -c.

4. Laboratories investigating primary production but not estimating pigments, should be asked to start this work in order to obtain as much information as possible on the relation between pigments and production.

5. The results already obtained indicate some areas of special interest. These areas should receive intensive study to elucidate the nature of the processes occurring. For this, it may be necessary before using the Richards-Thompson or chromatographic methods, to centrifuge large quantities (50 litres) of water so that adequate accuracy is obtained.

6. A field method should be developed for determining the amount of chlorophyll-a which is photosynthetically active.

7. Information is needed on the variation in pigment concentration in algae during the life cycle and in relation to external conditions of light, nutrients, etc.

SOME PROBLEMS IN THE ESTIMATION OF CHLOROPHYLL-A IN PHYTOPLANKTON

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INTRODUCTION

Recently there has been an increasing use of pigment estimations, particularly of chlorophyll-a, for assessing the abundance of planktonic algae. The most precise and reproducible methods have involved spectrophotometric measurements of absorbance (optical density) at one or more wavelengths, using extracts of the photosynthetic pigments in organic solvents. Of such spectrophotometric methods, that described by Richards and Thompson (1952) has been most widely followed, either directly or with small modifications. A variety of errors can affect this and related methods, and are discussed in several recent reviews (e.g., Lund and Talling, 1957; Krey, 1958a; Humphrey, 1959 and 1961). Here we wish to discuss (i) a probable error arising from the original calibration of the Richards and Thompson method for chlorophyll-a, (ii) the probable interrelations of results based upon similar measurements with different solvents, and (iii) a possible simplification in the method of calculation.

Divergencies in calibration

In the method of Richards and Thompson, the concentration of chlorophyll-a in a 90% acetone extract is determined principally from the absorbance in the red absorption maximum at 665 mμ, with small corrections based on the absorbances at 630 and 645 mμ. The absolute calibration (Richards, 1952) depends upon the values of specific absorption coefficients for chlorophyll-a in 90% aqueous acetone given by Zscheile (1934). The individual wavelengths for Zscheile's data, which were utilized for this purpose by Richards are not stated by the latter, but coefficients in the red spectral region of 660–665 mμ differ little between the two authors (Table 1). Unfortunately, considerable discrepancies exist in many determinations made before 1940 for the specific absorption coefficients of chlorophyll solutions (cf. Zscheile and Comar, 1941; Zscheile, Comar, and Mackinney, 1942; Rabinowitch, 1951, p. 603). After discussing this, Mackinney (1940) concluded that "the coefficients from five different laboratories are so incompatible that their application to spectroscopic assay of the green pigments s useless, until independent verification yields acceptable standards." We have been unable to find any later direct determinations for 90% acetone, but Vernon (1960) gives a single coefficient (see Table 1) obtained by comparison with the data of Smith and Benitez (1955) for solutions in ether. Both Mackinney (1941) and Zscheile et al., (1942) list similar specific absorption coefficients using 80% acetone for chlorophyll-a. Possibly one of the best samples of the latter was prepared by Mackinney, and was described by Zscheile, Comar and Harris (1944) as "a very excellent sample of dried chlorophyll-a." Coefficients obtained by these various workers are listed in Table 1. If the later values for 80% acetone solutions given by Mackinney, Zscheile, and coworkers are adopted, the earlier values of Zscheile (1934) for a 90% acetone solution imply that the latter shows an absorbance at 665 mμ which is 21% lower than the cor-

Table 1—Specific Absorption Coefficients (k), at Several Wavelengths Near the Red Absorption Maximum of Chlorophyll-a Solutions in Various Solvents

The coefficient k is defined by the relation $\log I_0/I = kc_a d$, where c_a is the concentration of chlorophyll-a in g/l, d is the path length or thickness of the solution in cm, I_0 the intensity of incident light and I that of light transmitted through the solution. The term ($d^{-1} \log I_0/I$) equals the absorbance per cm (D) used in Table 2.

Solvent	Authors	Wavelength (mμ) 660	662	663	664	665
100% acetone	Mackinney, 1940	–	–	84.0	–	–
?100% acetone	Holm, 1954	–	104.5	–	–	–
	Vernon, 1960	–	–	92.6	–	–
90% acetone	Zscheile, 1934, fig. 4*	67.5	–	68.4	–	64.0
	Richards, 1952, table 2	68.9	–	71.0	–	66.7
	Vernon, 1960	–	–	–	91.1	–
80% acetone	Mackinney, 1941	76.03	–	82.04	–	80.91
	Zscheile et al., 1942	76.0	–	82.0	–	–
		74.9	–	81.9	–	–
	Vernon, 1960	–	–	–	–	90.8
99.8% methanol	Mackinney, 1941	–	–	–	–	74.5
anhydrous ether	Zscheile, 1934, fig. 1	78	–	–	–	–
	Mackinney, 1941	90.1	–	–	–	–
	Zscheile & Comar, 1941	102.1	97.1	92.4	–	67.5
	Comar & Zscheile, 1942	102	–	–	–	–
	Zscheile et al., 1942	93.4	98.0	–	–	–
		98.4	99.7	–	–	–
	Koski, 1950	100.8	–	95.0	–	–
	Smith & Benitez, 1955	–	100.9	–	–	–
	Falk, 1958	93.8–98.0	97.3–100	–	–	–

*This figure can be read with only moderate precision.

responding absorbance of a solution in 80% acetone with an equal concentration of chlorophyll-a. If the data of Vernon (1960) for 80% acetone solutions are adopted, the difference is increased to 29.5%.

This large difference between the solvents appears unlikely from a variety of evidence. A direct comparison is described by Odum, McConnell, and Abbott (1958), who conclude that a change of solvent from 90% to 80% acetone is accompanied by an average 6% lowering of absorbance at 663 mμ. However their extracts were made from leaves containing chlorophyll-b, which would contribute slightly to absorbance at 663 mμ. We have made similar comparisons, at 660 and 665 mμ, of 80% and 90% acetone extracts from equal quantities of the plankton diatom Asterionella formosa Hass. We were unable to show an appreciable difference (>5%) between the corresponding absorbances. The data of Mackinney (1940 and 1941), reproduced in Table 1, indicate a specific absorption coefficient at 663 mμ which is only 2.3% lower in 80% acetone than in 100% acetone. Zscheile et al. (1944) observed that a change of solvent from 100% to 80% acetone caused the position of the red absorption maximum to move 2.5 mμ to the longer wavelengths, with a decrease in absorbance at 661.5 mμ of 6%, and a decrease in the maximum absorbance of 3% (a 2% decrease is indicated by the data of Vernon 1960). It is also possible that an increase in the water component may depress the solubility of other impurities (cf. Krey, 1958a). These findings, with the more detailed illustration by French and Elliott (1958) of the relative displacement in the red absorption maximum, also indicate that differences in absorbance at 665 mμ between solutions in 90% and 80% acetone are less than 6%, and probably less than 3%. Consequently if the later determinations of the specific absorption coefficients in 80% acetone are adopted, the value at 665 mμ used by Richards (1952) for 90% acetone is probably about 17% too low compared to data of Mackinney (1941) and Zscheile et al. (1942), and about 26% too low compared to the data of Vernon (1960). Vernon's data are supported by the independent estimation of chlorophyll-a from magnesium titration, a method also used by Falk (1958) for his data on solutions in ether.

Provisionally, we prefer to adopt an approximate intermediate value of 20% for the underestimate by Richards (1952) of the specific absorption coefficient at 665 mμ. In turn this would imply that the determinations of chlorophyll-a concentration by the equation set up by Richards and Thompson (1952) are probably about 25% too high, even in the most favorable conditions. for extracting chlorophyll-a by this method.

Measurements in solvents other than acetone

Comparative measurements in other solvents can be used for cross-reference between values of specific absorption coefficients, and may also have advantages for the extraction of pigments from the cells of certain algae. The most detailed information on the absorption coefficients for chlorophyll-a relates to solutions in anhydrous diethyl ether (cf. Table 1), and has been used to derive equations for estimating chlorophyll-a in mixtures containing chlorophyll-b (Comar and Zscheile, 1942; Koski, 1950; Smith and Benitez, 1955). Ether cannot be used directly for extracting pigments from algal cells, but a quantitative transfer can be made from another solvent such as acetone. We have made this transfer from two acetone extracts of pigments from cultured Asterionella cells, and compared estimates of chlorophyll-a based on the equations applicable to solutions in ether (noted above) with estimates on 90% acetone extracts according to the equation by Richards and Thompson (1952). Although the extracts from this diatom would contain chlorophyll-c, its contribution to the absorbance is unlikely to be appreciable (cf. Smith and Benitez, 1955, Fig. 5) at the principal wavelengths (above 660 mμ) involved in the measurements. The concentrations of chlorophyll-a calculated from the Richards and Thompson equation were approximately 40% higher than those obtained from the very similar results of the three calculations for solutions in ether. A corresponding percentage difference (about 48%) is indicated by the data of Holm (1954), who also compared absorbance in acetone extracts with the quantities of chlorophyll-a computed—after transfer to ether solution—according to the equation of Comar and Zscheile (1942).

Zscheile (1934, Fig. 1) also gives values of specific extinction coefficients of chlorophyll-a in ether. The importance value of 660 mμ, near the red absorption maximum, is clearly much lower than other more recent determinations (Table 1: also Zscheile and Comar 1941 Fig. 3). If adopted to calculate a concentration of chlorophyll-a from a measured absorbance, it would yield a value 25% higher than that obtained from the average (97.5) of the later values listed in Table 1. This average value is supported by estimates of chlorophyll-a derived from measurements of magnesium content (Falk, 1958), and is appreciably higher than the value given by Mackinney (1941), who may therefore have slightly overestimated concentrations of chlorophyll-a.

Methanol is the only other solvent which has been widely used for extracting chlorophyll from algal cells, and may be more efficient than acetone for this purpose when certain green and blue-green algae are involved (e.g., Gardiner, 1943; Steemann-Nielsen, 1961). In our experience 90% (aqueous) methanol has not been obviously more efficient than 90% acetone with planktonic blue-green algae in freshwaters; tests were made particularly with Oscillatoria agardhi var. isothrix and mixed phytoplankton from Lake Victoria (E. Africa). Using diatoms (Asterionella formosa and Melosira nyassensis) which decolorize rapidly in both these solvents, we have compared the absorbances obtained at 665 mμ in the red absorption maximum of chlorophyll-a. Cells were extracted for about 20 hours in the dark at about 6°C. For equal quantities of cells the absorbance in 90% acetone is usually a little higher (mean factor about 1.17) than the corresponding absorbance with 90% methanol. No significant difference could be found in a similar comparison using 90% and 100% methanol as solvents. These results are consistent with the data of Mackinney (1941) for specific absorption coefficients at 665 mμ for chlorophyll-a in 80% acetone and 99.8% methanol (Table 1), which are in the ratio 1.09 to 1, if the differences of absorbance between solutions in 80% and 90% acetone and in 90% and 100% methanol are small.

Equations used in calculations from spectrophotometric data

A number of equations of this type have been brought together in Table 2. They relate the required concentration (c_a) to the absorbance (D) at a wavelength at or near the red absorption

Table 2—Equations proposed for estimation of the concentration of chlorophyll-a (c_a, in mg/l), using measurements of absorbance (D, path length 1 cm) at the wavelengths indicated (in mμ) by subscripts.

Solvent	Source	Equation	No.
90% acetone	Richards & Thompson, 1952	$c_a = 15.6\ D_{665} - 2.0\ D_{645} - 0.8\ D_{630}$	(1)
	Modifications:		
	Odum et al., 1958	$c_a = 14.3\ D_{665}$	(2)
	Humphrey, 1961	$c_a = 15.6\ D_{665} - 1.8\ D_{645} - 1.3\ D_{630}$	(3)
80% acetone	Vernon, 1960	$c_a = 11.63\ D_{665} - 2.39\ D_{649}$	(4)
	Mackinney, 1941	$c_a = 12.7\ D_{663} - 2.69\ D_{645}$	(5)
(100%?) acetone	Holm, 1954	$c_a = 9.78\ D_{662} - 0.99\ E_{644}$	(6)
	Godnev & Sudnik, 1958	$c_a = 10\ D_{662} - 0.8\ D_{643}$	(7)
anhydrous ether	Comar & Zscheile, 1942	$c_a = 9.93\ D_{660} - 0.777\ D_{642.5}$	(8)
	Koski, 1950, as adapted by Norman, 1957	$c_a = 10.68\ D_{663} - 0.9506\ D_{644}$	(9)
	Smith & Benitez, 1955	$c_a = 10.1\ D_{662} - 1.01\ D_{644}$*	(10)

*Originally misprinted as 664.

Equations of a different type, useful for determining the total chlorophyll concentration in a mixture containing the a and b forms, are:

Solvent	Source	Equation	No.
anhydrous ether	Comar & Zscheile, 1942	$c_{a+b} = 7.12\ D_{660} + 16.8\ D_{642.5}$	(11)
		$c_{a+b} = 100.5$* D_{600}	(12)
80% acetone	Arnon, 1949	$c_{a+b} = 8.02\ D_{663} + 20.2\ D_{645}$	(13)
		$c_{a+b} = 29.0\ D_{652}$*	(14)
	Vernon, 1960	$c_{a+b} = 6.45\ D_{665} + 17.72\ D_{649}$	(15)

*Misprinted as 1/19.95 (= 50.1, if units of concentration are mg/l) in French, 1960.

maximum of chlorophyll-a, with one or two correction terms for the contribution to absorbance by other pigments which may be present in the extract. In most cases (equations 4 to 15) chlorophyll-b is the only other pigment, but the addition of chlorophyll-c should not appreciably alter the results of the calculations which depend principally on absorbance measured at wavelengths at 660 mμ or greater, where absorbance by chlorophyll-c is small. The equation of Richards and Thompson (1952) includes a small correction for chlorophyll-c. Where such absorbance by other pigments is small, the factor associated with the principal red absorbance is only a little greater than the reciprocal of the adopted specific absorption coefficient at the same wavelength, with obvious adjustment for the differing units of concentration (such as g/l and mg/l). Consequently this factor is considerably higher in the Richards and Thompson equation and its modifications (nos. 1-3) than in the four other equations relating to measurements in acetone solutions.

In applications of the Richards and Thompson equation, the result usually depends almost entirely on the absorbance measured at 665 mμ. Noting this, Odum et al. (1958) have proposed the simplified equation shown (Table 2, no. 2), which fitted well their observations on extracts from several algae and flowering plants. A very similar simplification, but with a proportionality factor of 14.9 instead of 14.3, can be fitted to our determinations with *Asterionella* and *Oscillatoria*, employing the Richards and Thompson equation. Odum et al. (1958) have introduced a further correction for supposed differences of solvent, but this appears to arise from a misreading of the sources of published data used by Richards and Thompson (1952). Possibly more acceptable but still rough approximations can be derived from our proportionality factor 14.9 (noted above), the suggested overestimate of 25% by the Richards and Thompson equation, and our comparison of absorbance at 665 mμ in 90% acetone and 90% methanol extracts.

These approximate relations are

$$c_a = 11.9\ D_{665}\ \text{(90\% acetone)}$$

and

$$c_a = 13.9\ D_{665}\ \text{(90\% methanol)}$$

Summarizing, the calculation of chlorophyll-a concentration by the Richards and Thompson equation is probably affected by a markedly incorrect specific absorption coefficient. Only an approximate indication of the probable error from the calculation—about +25%—can be given here, and there is some evidence (especially from Vernon, 1960) that the error may be slightly larger. Probably greater differences and errors can easily arise, as between the use of "wet" and "dry" preparations of chlorophyll-a, and in the various modifications of the Richards and Thompson procedure of preparing extracts (cf. Humphrey, 1958 and 1961), the presence of pheophytins in extracts from natural populations, the incomplete extraction of the algal cells, and possibly unavoidable errors in work on pigment mixtures (cf. Norman, 1957). However, such variation does not excuse the perpetuation of purely formal differences of calculation, which may affect the same algal material (e.g., Asterionella: Talling, 1957 and 1960b); further standardization is very desirable. As pointed out by Davis (1957), this can be achieved by adopting revised values of specific absorption coefficients, rather than by independent calibrations with even the best commercial samples of chlorophyll-a which can lead to appreciable errors (cf. Zscheile and Comar, 1941; Falk, 1958).

PHYSIOLOGICAL FACTORS AFFECTING THE INTERPRETATION OF PHYTOPLANKTON PRODUCTION MEASUREMENTS

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ABSTRACT

Although other methods have been used to measure phytoplankton production, this paper discusses only the physiological factors which affect the interpretation of carbon-14 measurements of production. In principle, gross or "real" photosynthesis will be measured by the carbon-14 method if the following conditions are met: (1) carbon-14 is assimilated at the same rate as carbon-12; (2) no carbon-14 is incorporated by processes other than photosynthesis; (3) no assimilated carbon-14 is lost by excretion; and (4) no carbon-14 is lost by respiration which accompanies photosynthesis. In practice, none of these conditions is completely satisfied, but the data may be corrected for deviations from these conditions.

The correction for the difference in the rate of assimilation of the two isotopes (1, above) has been ascertained at plus 6 per cent. The correction for non-photosynthetic uptake of carbon-14 (2, above) may be made by incubating a darkened aliquot simultaneously with an illuminated one. Further studies are needed on the excretion (3, above) of organic matter by marine phytoplankton. This correction is probably small, but may depend upon incubation and nutrient conditions.

To correct for respiration (4, above), the ratio of photosynthesis to respiration (P/R) and the amount of intermixing between the two processes must be known. If 100 per cent of the respiratory CO_2 is preferentially reutilized in photosynthesis, and no respiratory correction is made, the carbon-14 method will measure net photosynthesis. Early tests of this concept measured photoinhibition of the respiratory release of $C^{14}O_2$ from labeled cells. Comparisons were also made between carbon-14 uptake (uncorrected for respiration) and net O_2 evolution under various illumination and nutrient conditions. More recently, carbon-14 uptake has been compared with growth.

Under conditions of saturating light intensities and adequate intracellular nutrient levels, net O_2 evolution differs very little from gross O_2 evolution (the respiration correction is small) and carbon-14 uptake agrees with both measurements within experimental error. In cultures maintained under such conditions, logarithmic growth constants, calculated from increases in cell concentration or other growth measurements, are statistically equivalent to similar constants calculated from carbon-14 uptake or net O_2 evolution rates and organic carbon analyses.

At subsaturating light intensities, carbon-14 uptake is equivalent to or is less than net O_2 evolution, and this relationship obtains down to the compensation intensity for O_2 evolution. At or below the compensation intensity, carbon-14 uptake more closely approximates gross O_2 production, but the values are very uncertain.

In incipiently nutrient-deficient algal cultures, net O_2 evolution also does not differ significantly from gross O_2 evolution; carbon-14 assimilation (uncorrected for respiration) is equivalent to either net or gross O_2 production. Growth constants decrease as deficiency progresses, but constants calculated from either O_2 evolution or carbon-14 uptake are equivalent to those calculated from growth measurements.

In extremely deficient cultures (at P/R ratios down to 2), carbon-14 uptake (uncorrected for respiration) agrees with net O_2 evolution and differs greatly from gross O_2 evolution. As deficiency progresses, the P/R ratio decreases even more, and gross O_2 evolution may become less than respiration. Comparisons of carbon-14 uptake and O_2 evolution are inconclusive under such extreme conditions. Such conditions have little oceanographic significance, since a natural population could not persist at P/R ratios less than 2.

These results are discussed in relation to nutrient and illumination conditions which might be present in the sea. Under most conditions, the carbon-14 method (uncorrected for respiration) appears to measure a net process, such as algal growth or net O_2 evolution.

INTRODUCTION

Several different methods have been developed for the measurement of phytoplankton production in the sea. Because of its great sensitivity, the carbon-14 method of Steemann-Nielsen (1952) has come into the widest use, and most marine biological laboratories are now making intensive studies of carbon-14 uptake by phytoplankton in their regions of interest. All methods of measuring phytoplankton production and various other aspects of algal growth and physiology were comprehensively discussed in an excellent review by Strickland (1960). The reader is referred to that paper for more detailed treatment than can be given here.

When the carbon-14 method was first used during the cruise of the Galathea around the world, the values for one area—the Sargasso Sea—were 10-200 times less than previous values obtained with the oxygen method by Riley, et al. (1949). This discrepancy led to a great deal of controversy regarding just what was measured by the carbon-14 method. Workers at Woods Hole (Ryther, 1954b and 1956b) claimed that the method measured net production, while Steemann-Nielsen maintained that the data, when certain corrections were introduced, are equivalent to gross production. One of the purposes of the present paper is to examine and review these corrections, and the physiological factors affecting them.

This controversy has led workers in some laboratories to wonder whether the carbon-14 method was an adequate measure of an increase in algal biomass. Another purpose of this paper is to summarize recent results comparing carbon-14 uptake with growth in algal cultures.

In principle, gross or total photosynthesis will be measured by the carbon-14 method if the following conditions are met: (1) carbon-14 is assimilated at the same rate as the stable isotope of carbon, carbon-12; (2) no carbon-14 is incorporated by the processes other than photosynthesis; (3) no assimilated carbon-14 is lost by excretion or autolysis during the incubation, or by rupture of cells during filtration; and (4) no assimilated carbon-14 is lost by the intermixing of respiration with photosynthesis. However, in practice, none of these conditions is completely satisfied, and if gross photosynthesis is to be calculated, the raw data must be corrected for deviations from them.

CORRECTIONS FOR CARBON-FOURTEEN DATA

The Isotope Effect

Theoretically, because $C^{14}O_2$ has a molecular weight which is 4.5% heavier than that of $C^{12}O_2$, assimilation of $C^{14}O_2$ should proceed at a proportionally slower rate than that of $C^{12}O_2$. Early estimates of this isotope effect in photosynthesis indicated that $C^{14}O_2$ was assimilated approximately 15% more slowly than $C^{12}O_2$ (Weigle, Warrington, and Calvin, 1951; Van Norman and Brown, 1952). In these experiments the concentration of these isotopes was recorded automatically during periods of photosynthesis lasting about 30 minutes. After 30 minutes, the concentration of CO_2 had decreased to nearly zero and photosynthesis had nearly ceased. The

isotope effect was measured during the period when photosynthesis proceeded at a constant and high rate. These studies, while technically very elegant, did not yield unequivocal determinations of the magnitude of the isotope effect. Experimental errors were large and the corrections applied to the data for dark uptake (exchange) and respiration were also large (cf. Craig, 1954; Steemann-Nielsen, 1955b). Furthermore, the half-hour period is much shorter than that used in routine productivity measurements.

In his original paper Steemann-Nielsen (1952) used a value of 6% to correct for the isotope effect. He also recalculated Van Norman and Brown's results and found a value of 5% (Steemann-Nielsen, 1955b).

More recently, Buchanan et al. (1953) and Sorokin (1960) compared specific activities (cpm/carbon concentration) in Scenedesmus cells with specific activities of the medium following several weeks of growth in labeled medium. In both studies the specific activity of the algae was 6.5% less than that of the medium, and the experimental error was much less than in previous determinations.

These two types of experiments may give different results because the experimental times were greatly different. Short-time experiments refer to photosynthesis whereas long-term experiments may include isotope fractionation in all of the many biochemical reactions in which carbon participates. The isotope effect could be determined using incubation periods comparable to those normally used in productivity studies by comparing pH changes in dense cultures with carbon-14 uptake. This was attempted by Thomas (unpublished data), but experimental errors were too large. If these errors are ignored, the effect is about 9% during a 4-hour photosynthetic period, a value which is intermediate between short-term results and those obtained during long-term algal growth. More effort is needed to reduce the error in such comparisons, and the use of high-precision pH meters and more precise counting methods than Geiger counting may provide unequivocal values for the isotope effect. Until more precise measurements are made, which are also comparable to the usual productivity measurement, a factor of 5% appears reasonable to use in routine surveys of phytoplankton production.

Non-Photosynthetic Assimilation of Carbon-14

During incubation of algae with carbon-14, a certain amount of the tracer will be taken up by processes other than photosynthesis. In his original description of the method, Steemann-Nielsen (1952) subtracted one percent from the radioactivity taken up by light-saturated phytoplankton to correct for non-photosynthetic assimilation. In healthy algal cultures, fixation of carbon-14 in the dark is similar to the one percent value applied by Steemann-Nielsen (Brown et al., 1949; Thomas, unpublished). However, under conditions of extreme nitrogen deficiency, assimilation in darkened cultures may reach 37% of that in illuminated cultures (Steemann-Nielsen and Al Kholy, 1956). A similar high value for dark fixation was not found for phosphate-deficient cultures. If such an increase in relative dark uptake were characteristic of nitrogen-deficient algae in general, measurements of dark uptake might be a useful index of the nitrogen status of natural populations. This hypothesis needs to be substantiated. Perhaps the nitrogen/carbon ratio or carotenoid/chlorophyll ratio of cultures or natural populations can be correlated with relative dark uptake.

In natural populations, dark fixation can be greater than a few percent of the value for photosynthetic fixation of carbon-14 (Doty, 1958a; Holmes, 1958b; Thomas and Simmons, 1960). Detailed recent measurements by Steemann-Nielsen (1960a) of assimilation in darkened bottles showed that it could be as high as 9% of assimilation in the light for surface samples and up to 30% for samples from deep water. However, most of the values were 1 to 3%.

In view of these variations and the possible effects of varying intracellular nutritional status, it seems unwise to apply a standard correction for dark uptake uniformly to all samples during routine productivity surveys. Wherever possible, darkened bottles should be incubated with illuminated ones to establish an empirical correction.

Losses of Labeled Carbon by Excretion or Rupture of Cells During Filtration

As $C^{14}O_2$ is taken up during incubation and converted into labeled organic matter, some of it may be excreted and go into solution outside the cell. Similarly, if a cell containing labeled

organic matter were to die and rupture during incubation or filtration, part of the radioactivity would be lost. The carbon-14 method underestimates total photosynthesis to the extent that excretion or rupture occurs. Most investigators of marine productivity have neglected such losses since early studies of algal excretion indicated that about 95% of the carbon in healthy cultures was contained within the cells (Myers and Johnson, 1949, and others). However, more recent investigations have indicated that appreciable amounts of carbon can be excreted from algal cells (Allen, 1956; Guillard and Wangersky, 1958).

Using carbon-14, Fogg (1958) measured excretion and photosynthesis by natural populations in two Swedish lakes. After incubation with carbon-14 *in situ* and filtration, he removed the excess radioactive carbon dioxide from the filtrate by acidification and aeration, and evaporated the filtrate to dryness. The residue was extracted with ethanol and the extract tested for radioactivity. In all samples, some radioactivity was found in the extract. Fogg expressed this activity as a fraction of that retained by the filter. In surface samples from the eutrophic Lake Erken, the excreted activity was only 2% of that retained by the filter. At 10 meters it had increased to 8%, and was 21% in a dark bottle control from 10 meters. The relative excreted activity in samples from the oligotrophic Torneträsk was somewhat greater than in samples from Lake Erken. The samples from Torneträsk were incubated for 40 hours in rainy weather; those from Erken were incubated for 24 hours in overcast weather.

These results show that excretion may be affected by light intensity, since excretion increased with increasing depth. Excretion was also greater in an oligotrophic lake as compared with a eutrophic lake, a result which might be attributed to nutrient deficiency, although illumination conditions were also different. With regard to the effects of deficiency it might be mentioned that Guillard and Wangersky (1958) found maximum quantities of extra-cellular carbohydrates in senescent cultures of marine flagellates. Such cultures presumably could have been nutrient-limited. Similarly, excreted radioactivity (that which passed a PH Millipore filter) was found in old cultures of carbon-14-labelled *Dunaliella primolecta*, but not in young cultures (Lasker and Holmes, 1957).

Lasker and Holmes also investigated the relative retention of radioactivity from labelled *Dunaliella* cultures by different filters. AA Millipore filters (pore size 0.8 μ) generally retained less radioactivity than HA filters (pore size 0.5 μ) or PH filters (pore size 0.30 μ). With *Dunaliella*, HA and PH filters retained equivalent amounts of activity. Holmes and Anderson (cf. Holmes, 1961b) have continued to investigate retention by different filters, using labeled natural populations from the Friday Harbor vicinity. Many successive experiments in July and August 1960 showed that generally the PH filter retained more activity than the HA filter. The average increase in retention was 30%, but this increase varied considerably from experiment to experiment. In five experiments where the GS filter (pore size 0.22 μ) was compared with the PH filter, the GS retained more activity than the PH. However, during a recent Scripps cruise to tropical waters, the GS did not always retain more activity than the PH (Holmes, personal communication). Since the porosities of the PH and GS filters are less than the sizes of all known photosynthetic organisms, it appears that the cells are rupturing during filtration and fragments are retained by the filters. This view is supported by recent experiments with natural populations off the Oregon coast which showed that, for a filter of a given porosity, retention was inversely related to the amount of vacuum used in filtration (Anderson and Holmes, personal communication).

More knowledge is now needed of just how fine a filter is necessary to retain all or most of the radioactivity from carbon-14-labelled natural populations, and also what negative pressure should be used for filtrations. We need to know whether the PH filter (now used routinely at Scripps Institution of Oceanography and the University of Washington) is capable to retaining a constant proportion of the total radioactivity. The approaches of Fogg and of Holmes and Anderson could profitably be combined in a single investigation comparing retention by various filters with the amount of activity passed by each filter. Further definition of the effects of light intensity or intracellular nutrient status on excretion is also needed. The results of Fogg and Guillard and Wangersky provide preliminary evidence that such factors will affect excretion.

Respiratory Losses of Labelled Carbon

The application of a correction for respiration that accompanies photosynthesis remains somewhat uncertain. This correction is dependent upon the rate of respiration relative to that of gross or total photosynthesis. For healthy algal cells incubated at high light intensities, respiration is about 10% of photosynthesis. As the intensity decreases below saturation, the ratio of photosynthesis to respiration also decreases. The P/R ratio also decreases as cells become nutrient-deficient (Ryther, 1954b; Thomas, unpublished). In natural marine populations, respiration was 15% (or less) of the light-saturated rate of photosynthesis in 90% of some 78 determinations made by Steemann-Nielsen and Hansen (1959a), off Greenland. It is probable that in nature, respiration rarely exceeds 50% of photosynthesis, since, assuming 12 hours of daylight, photosynthesis must be twice respiration to balance the loss of carbon from the algae during the night. Otherwise the phytoplankton population would not persist (Steemann-Nielsen and Al Kholy, 1956; Strickland, 1960).

The other factor which enters into the application of a correction for respiration is the extent of intermixing of respiration with photosynthesis. This subject was reviewed by Rabinowitch (1956), but the magnitude of intermixing and its mechanism remain somewhat obscure. The nature of the mechanism of intermixing (be it inhibition of respiration, respiration of previously labeled organic matter, a preferential reutilization of respired CO_2, etc.) is of interest to the physiologist; the ecologist who applies the carbon-14 method needs only to know the magnitude of the correction, if any, that he should apply to raw carbon-14 data to determine total photosynthesis, but even this is uncertain and variable.

The first workers to apply isotopic tracers to this problem, Weigle, Warrington, and Calvin (1951), measured changes in total CO_2 and radioactive CO_2 during the incubation of barley leaves for alternating dark and light periods. From these changes they calculated changes in specific radioactivity which could only be explained by postulating that respiration in the light was only 50% of that in darkness. Using a recording mass spectrometer to measure changes in oxygen isotopes in a Chlorella suspension during alternate light and dark periods, Brown (1953) generally found no change in oxygen uptake due to light. Results with the blue-green alga, Anabaena, were less conclusive, and ranged from nearly complete inhibition at low oxygen tensions to a two and one-half fold stimulation at high light intensities and high oxygen tensions (Brown and Webster, 1953).

It may be argued that measurements of changes in oxygen uptake have little to do with the possible losses of tracer carbon during a productivity measurement. Thus, the data of Steemann-Nielsen (1955b) and of Ryther (1956c), are perhaps more applicable. The loss of carbon-14 from previously labeled algae was measured in the light and in darkness. Steemann-Nielsen labeled Chlorella for one and one-half hours, and transferred the cells to non-radioactive medium. During incubation periods of up to a further seven hours, he found that the amount of tracer released in the light was only 30-40% of that released in darkness. Ryther grew Dunaliella cells for several days in a medium containing carbon-14. He then transferred the cells to a non-radioactive medium and incubated them in the light and in darkness for 24 hours. Illumination completely suppressed the release of carbon-14 from the cells. More recent studies with a recording mass spectrometer and carbon isotopes tend to support the contention of Steemann-Nielsen that release of CO_2 is not completely inhibited by light. Brown and Weis (1959) showed that the production of CO_2 by Ankistrodesmus was inhibited about 50% by light, and that this inhibition was independent of light intensity. Similar results were obtained using Ochromonas cultures. (Weis and Brown, 1959).

If no $C^{14}O_2$ is released to the external medium at all, one can assume that respiratory $C^{14}O_2$ is being taken up preferentially within the cell, and reutilized in photosynthesis. Thus less carbon-14 will be taken up from the external medium and the method will measure net photosynthesis. If only part of the respiratory $C^{14}O_2$ is reutilized then the carbon-14 measurement will be equivalent to some value between net and gross photosynthesis. The crucial aspect of the correction for respiration is the P/R ratio, and the amount of intermixing of the two processes is of less importance. In Table 1, two sets of correction factors for respiration, by which raw carbon-14 data may be multiplied to obtain gross photosynthesis, are calculated. One set of factors is calculated assuming complete photoinhibition of respiratory

Table 1 — Factors to Correct Carbon-14 Data for Respiration in Order to Obtain a Value for Gross Photosynthesis

P/R Ratio	Calculated according to Ryther (100% photoinhibition)	Calculated according to Steemann-Nielsen (60% photoinhibition)
20	1.05	1.03
10	1.10	1.06
5	1.20	1.12
3	1.33	1.20
2	1.50	1.30
1.5	1.67	1.40
1	2.00	1.60

$C^{14}O_2$ release (Ryther, 1956c); the other set is calculated assuming 60% photoinhibition (Steemann-Nielsen, 1955b). Note that the difference between the two factors is excessive only at P/R ratios of less than 2.

GENERAL REMARKS ON THE COMPARISONS OF THE CARBON-14 METHOD WITH O_2 EVOLUTION AND WITH GROWTH

In the above discussion of corrections that may be applied to raw carbon-14 data, most of the evidence was direct; changes in the carbon-14 content of algal cells or in the rate of uptake of carbon-14 were described. The method has also been compared with other methods of measuring the rate of increase of cell material, i.e., with the O_2 method of measuring photosynthesis and with various measurements of algal growth. Any such comparison is less direct and is dependent upon an assessment of the over-all error of each method.

The carbon-14 method, in our laboratory, has an over-all precision of approximately ±15%. The standard error (sampling and counting error) of the uptake of radioactivity by 10 replicate cultures incubated under identical conditions was ±7%; the error in determining the amount of radioactivity added (by extrapolating our self-absorption curve to zero) was ±4%; and the error in measuring the total CO_2 content of the suspending medium was ±6%. Pooling these three sources of error gives an over-all value of ±15%. In the field, the sampling error will generally be greater than ±7% (cf. Holmes, Schaefer, and Shimade, 1958; Cassie, this volume). The use of very precise methods of measuring radioactivity and CO_2 content would probably reduce the over-all error, even in the laboratory, by only one-half, and the additional time and expense seem hardly worth the effort, except for possibly making more precise estimates of the isotope effect.

In our hands, the precision of measurements of net and gross O_2 evolution is about ±4%, providing the results are only expressed in ml. O_2/liter/hours. However, for comparison with carbon-14 uptake, the O_2 values must be converted to equivalent carbon production. For this conversion, a photosynthetic quotient must be selected that may vary as much as ±12% depending on nutritional or illumination conditions (Ryther, 1956b). Thus, the over-all error is nearly as much—±13%—as that of the carbon-14 method.

Growth in an algal culture—and sometimes in nature (Verduin, 1952b)—proceeds in a logarithmic fashion until such time as the culture becomes so dense that nutrients are depleted or illumination within the culture is reduced by mutual shading. Logarithmic growth can be expressed by the following equation:

$$K_2 = \frac{\log_2 C_2 - \log_2 C_1}{t_2 - t_1}$$

where C_2 and C_1 are concentrations of cell material at times t_2 and t_1. K_2 is the reciprocal of the time taken for the population to double, providing logarithms to the base 2 are used ($\log_2 = 3.32 \times \log_{10}$). This time can be called the generation time. C_2 and C_1 can be measured to various ways: cell concentration, optical density, cell carbon or nitrogen, dry weight, etc.

To compare photosynthesis with growth, it is necessary that C_1 be measured before the photosynthetic period and expressed in the same units as photosynthesis. Then a photosynthetic K_2 value can be calculated and compared with the K_2 determined from growth measurements. Suppose that a culture containing 32 mg. organic carbon per liter is photosynthesizing at a rate of 1 mg C/liter/hour. The calculation of a photosynthetic K_2 value is shown in Table 2. K_2 values calculated from growth or photosynthesis measurements are subject to the experimental error of both C_1 and C_2, and are therefore somewhat less precise than either C_1, or C_2 or the rate of photosynthesis. The comparison of growth with photosynthesis is thus made on a statistical basis.

Table 2—Sample Calculation of a Photosynthetic K_2 Value

C_1 = 32 mg. C/L   Photosynthesis = 1 mg. C/L/hour

C_2 = 32 + 1 = 33 mg. C/L

$t_1 = 0$

$t_2 = 1$

$$K_2 = \frac{3.32 \log_{10} 33 - 3.32 \log_{10} 32}{1} = \frac{3.32\,(1.51851 - 1.50515)}{1}$$

$$= 0.0444 \text{ hours}^{-1}$$

Generation time = 1/0.0444 = 22.5 hours

THE EFFECT OF LIGHT

Corrections and Comparisons at Saturating Light Intensities

Assuming that saturation of photosynthesis occurs at an illuminance of 2000 foot-candles (cf. Ryther, 1956a), saturating intensities will occur at an optical depth of 20% at noon on a bright day and near the surface of a dull day. The saturation intensity will vary with the species composition of the phytoplankton population (Ryther, 1956a) and with its previous history of illumination (Ryther and Menzel, 1959; Steemann-Nielsen and Hansen, 1959b). Ideally, to estimate illumination conditions during a carbon-14 measurement, each investigator should make his own light saturation and species composition studies of the population(s) with which he is dealing. Then he can make a more precise estimate of corrections to apply to obtain gross photosynthesis values.

At saturating intensities, the P/R ratio will be 10-20, and these corrections will be relatively small, +5% for the isotope effect, –1% for dark uptake (assuming no dark bottle), +3% for excretion (assuming no rupture of cells on the filter pad), and +5-10% for respiration. The overall correction will be about +15% and is roughly equivalent to the experimental error of the carbon-14 method.

Since the P/R ratio is relatively great, gross photosynthesis will not differ greatly from net photosynthesis, and under such conditions carbon-14 uptake does not differ significantly from either net or gross O_2 evolution. Good agreement between gross O_2 production and carbon-14 uptake at 1000 foot-candles was first demonstrated by Ryther and Vaccaro (1954) using both Nitzschia cultures and natural populations in coastal sea water. Equivalence between net O_2 evolution and carbon-14 uptake at saturation was later shown by Ryther (1956b), and this is shown in Figure 1. In this experiment, gross O_2 production differed so greatly from net production (the P/R ratio was about 2) that one suspects that the culture was nutrient deficient. More realistic comparisons ($P/R \cong 5$) were made by Ichimura and Saijo (1958) and are reproduced in Figures 2 and 3. Considering the uncertainties in the photosynthetic quotient (these authors used 1.0) and in dark uptake, the carbon-14 results appear to agree with both

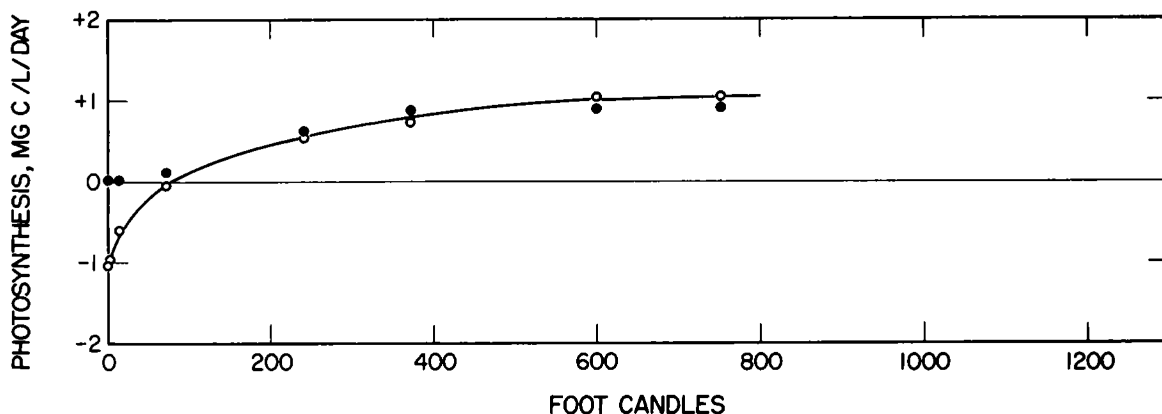

Fig. 1—Photosynthesis measured by net oxygen production (open circles) and carbon-14 uptake (filled circles) as a function of light intensity in a pure culture of Dunaliella euchlora. (Reproduced from Ryther, 1956).

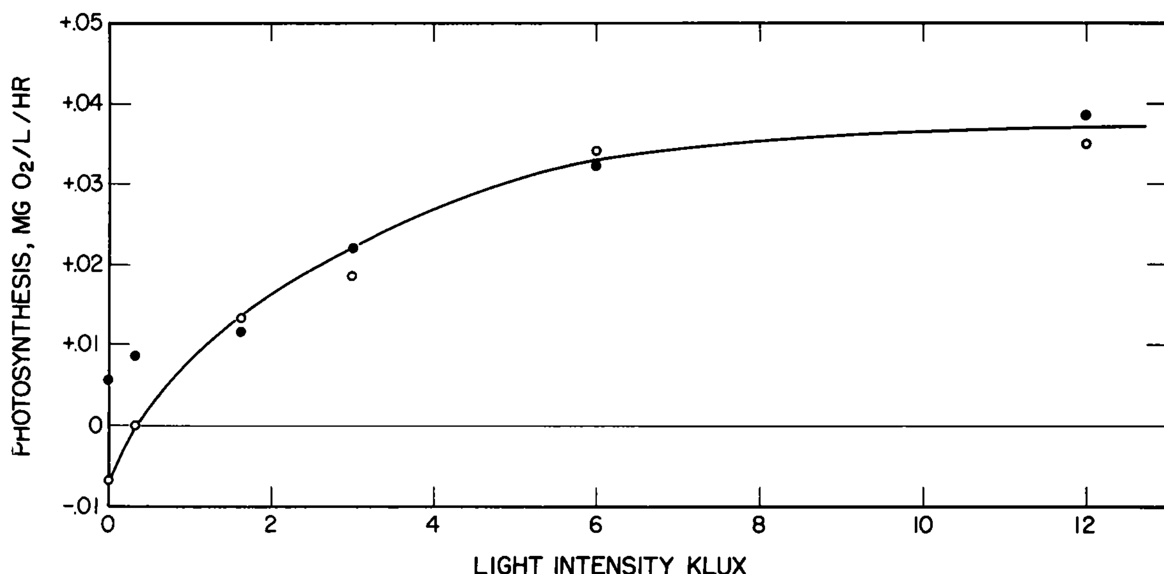

Fig. 2—Photosynthesis measured by oxygen production (open circles) and carbon-14 uptake (filled circles) in a pure culture of Chlorella sp. (Reproduced from Ichimura and Saijo, 1958).

net or gross O_2 evolution at saturating illuminances, although most carbon-14 values were closer to net O_2 production.

In our laboratory, we have been using cultures of Dunaliella primolecta for extensive comparisons of carbon-14 uptake with O_2 evolution and growth. (Thomas, unpublished). In 35 comparisons of carbon-14 uptake and O_2 evolution at saturating light intensities, carbon-14 uptake was 101 ±23% of net O_2 evolution and 83 ±19% of gross O_2 evolution. These carbon-14 data were corrected for isotope effect and dark uptake, but not for respiration or excretion. In 20 determinations where photosynthetic capacity (photosynthesis/cell) was determined, no significant differences were found between capacities determined from carbon-14 uptake, net O_2 evolution, or gross O_2 evolution.

To compare growth with photosynthesis, we grew Dunaliella in a 40-liter aquarium which was illuminated from below with a bank of fluorescent lights. Samples were taken from the culture at various intervals for measurements of cell material and aliquots of each sample were also dispensed into glass-stoppered bottles for photosynthesis measurements. The bottles were placed on the bottom of the culture itself in an attempt to ensure that conditions were the same for photosynthesis as for growth.

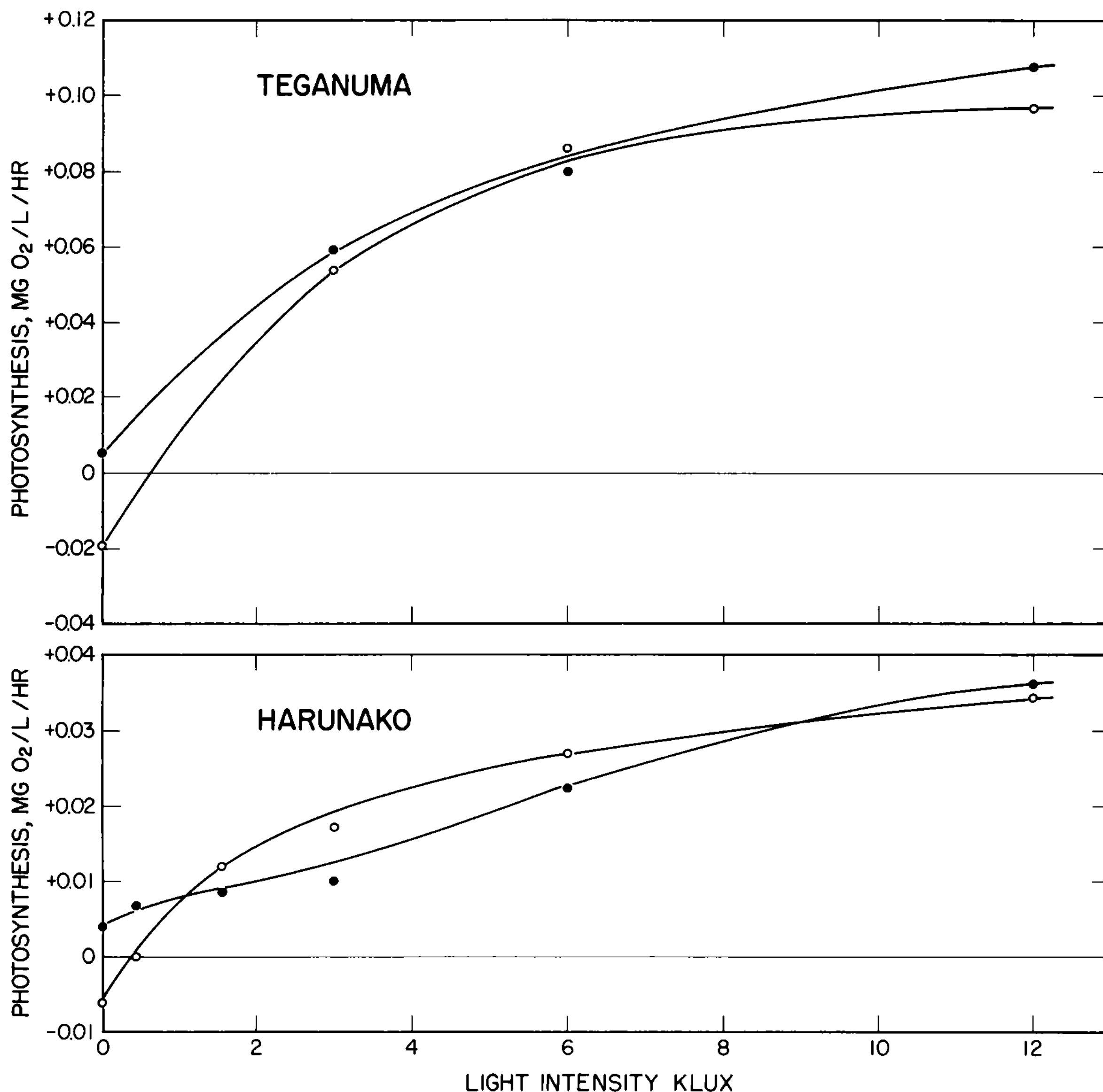

Fig. 3 — Photosynthesis measured by O_2 (open circles) and carbon-14 (filled circles) methods in water samples taken from the eutrophic Lake Teganuma and the mesotrophic Lake Harunako. (Reproduced from Ichimura and Saijo, 1958).

When we first made this comparison, we found that the K_2 values calculated for growth in the whole culture were 30-40% less than those calculated for photosynthetic bottles placed in the bottom of the culture. This is shown in Figure 4. The difference between K_2 values for growth and photosynthesis was statistically significant ($p < 0.01$) and was attributed to a difference in illumination between the bottles and the culture as a whole. When this experiment was repeated with a culture that was less dense, the mean K_2 value for photosynthesis was 0.0945 hours^{-1}, while that for growth was 0.0835 hours^{-1}. This difference was not significant and photosynthesis as measured by net O_2 production and carbon-14 uptake was equivalent to growth. Rough calculations indicated that illuminances in bottles and in the culture did not differ more than about 10%.

Carbon-14 Measurements at Subsaturating Light Intensities

As light intensities decrease below saturation, the various corrections increase and the validity of the carbon-14 method becomes less certain. The correction for the isotope effect

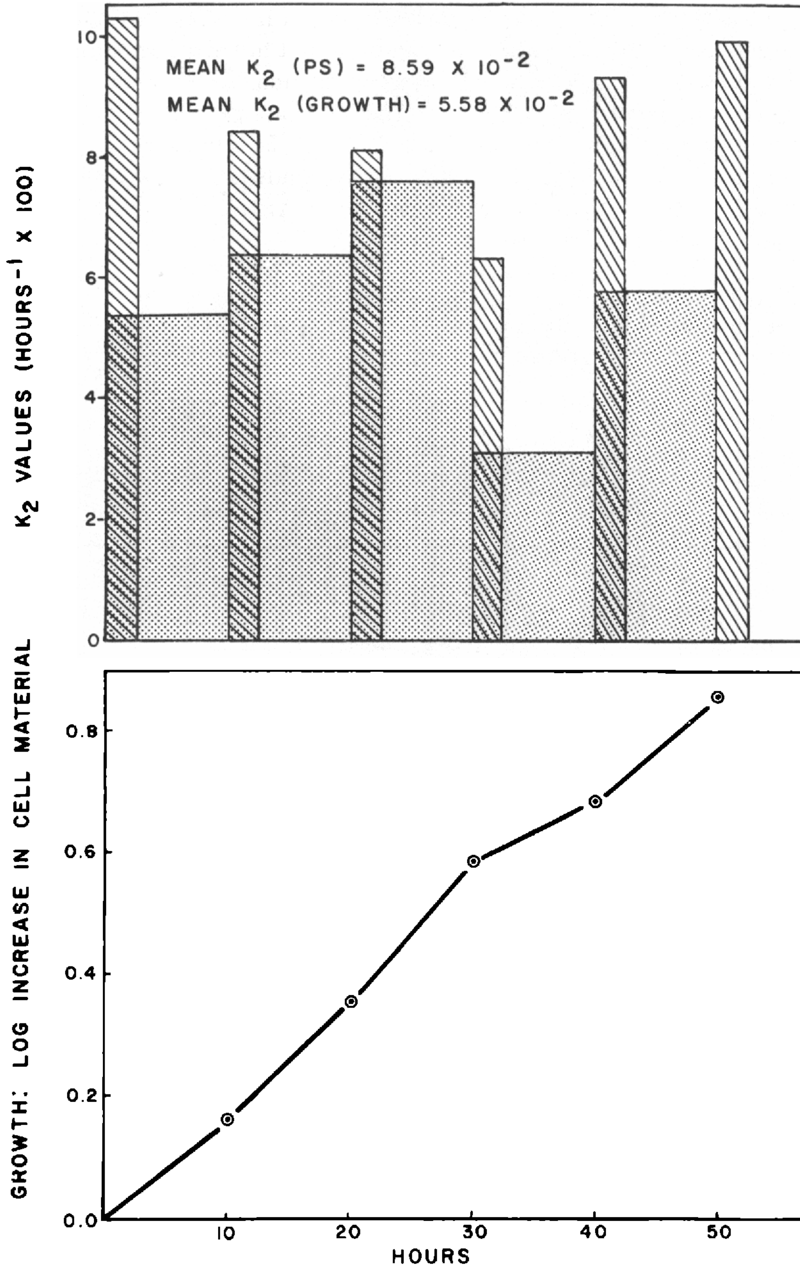

Fig. 4—Comparison of growth and photosynthesis in a culture of Dunaliella primolecta. The upper figure compares photosynthetic K_2 values (hatched bars) made at 10-hour intervals with K_2 values (stipled bars) calculated from increases in all material during each 10-hour interval. The lower figure shows the growth of the culture as measured by increases in cell concentration, optical density, organic nitrogen, organic carbon, and dry weight. The increase in each growth parameter was calculated relative to that at the beginning of the experiment; the points represent the logarithms of the mean of these relative increases.

presumably remains constant. Dark uptake is relatively more important and dark bottles should certainly be incubated with illuminated ones. Excretion of carbon-14 may also increase with decreasing light intensity, as is indicated in the experiments reported by Fogg (1958). With decreasing light intensity the P/R ratio decreases and the respiratory correction becomes very important. The estimated corrections that can be applied to obtain net or gross photosynthesis at three different light intensities are shown in Table 3. It should be emphasized that these values are only estimates, and indicate that uncertainties are relatively great at the compensation intensity. It is assumed that a correction for dark uptake was made with a dark bottle. Roughly, one could multiply raw carbon-14 data by 1.15, 1.25, and 2.0 to obtain gross phytosynthesis at the three intensities given in Table 3; similarly, use of the factors 1.05, 1.05, and 1.0 would give rough values for net photosynthesis. In any case such rough values would probably not differ from the true value by an amount greater than the overall experimental and sampling error.

Table 3 — Corrections to Apply to Raw Carbon-14 Data to Obtain Net and Gross Photosynthesis at Three Different Light Intensities

	Intensity		
Estimated Correction for:	Saturation (P/R = 10)	Half Saturation (P/R = 5)	Compensation (P/R = 1)
Isotope Effect	+5%	+5%	+5%
Excretion	+2%	+5%	+10%
Respiration (Ryther Correction)	+10	+20	+100
Respiration (Steemann-Nielsen Correction)	+6	+12	+60
Total Correction for Gross Photosynthesis (after Ryther)	+17%	+30%	+115%
Total Correction for Gross Photosynthesis (after Steemann-Nielsen)	+13%	+22%	+75%
Total Correction for Net Photosynthesis (after Ryther)	+7%	+10%	+15%
Total Correction for Net Photosynthesis (after Steemann-Nielsen)	+3%	+2%	−25%

Comparisons of carbon-14 uptake (uncorrected for respiration) with net O_2 production at subsaturating intensities (Ryther, 1956b) indicated that the two measurements were comparable down to the compensation intensity (Fig. 1). The data of Ichimura and Saijo (1958) are even more convincing evidence that carbon-14 uptake is equivalent to net O_2 production (Fig. 2; Fig. 3), especially if their data are corrected for dark uptake. However, carbon-14 uptake is less than net O_2 production at intensities that are one-half to one-quarter of saturating for Lake Harunako. Carbon-14 uptake is greater than net O_2 production at the compensation point.

In preliminary experiments (Thomas, unpublished), we also found that uncorrected carbon-14 uptake at or below the compensation point for net O_2 evolution was greater than net O_2 evolution, and that photosynthetic tracer fixation was greater than dark fixation. However, at such low intensities, as is indicated in Tables 1 and 3, all corrections become so much more uncertain, that one cannot attach much significance to carbon-14 data.

INTRACELLULAR NUTRIENT LEVEL

The Effects of Incipient Nutrient Deficiency on Carbon-14 Measurements

When healthy algal cells are transferred to a nutrient-deficient medium, the intracellular concentration of the nutrient decreases. In nitrogen-deficient Scenedesmus, this decrease was exponential with time and a minimum level (one-fourth the normal concentration) was reached after about 5 days of deficiency (Thomas and Krauss, 1955). With nitrogen-deficiency, a period

of incipient deficiency, when the concentration within the cells dropped rapidly, could be distinguished from extreme deficiency, when a minimum nutrient level was reached. When Scenedesmus cells were transferred to phosphorus-deficient medium, the decrease in intracellular phosphorus was not so rapid as with nitrogen deficiency. After 11 days of phosphate deficiency, the cells still contained half the original phosphorus (Thomas, 1954). Incipient phosphorus-deficiency is less easily distinguished from extreme deficiency. Arbitrarily we can suggest that the first few days of deficiency of a nutrient represent incipient deficiency, as contrasted with extreme deficiency. Extreme deficiency is characterized by minimal intracellular nutrient levels, and occurs after these first days.

Assuming that deficiency has little or no influence on correction of carbon-14 data for the isotope effect, we can proceed to examine the effects of deficiency on the other corrections. A correction for dark uptake should be made by incubating a separate darkened bottle. This is especially important if nitrogen deficiency is suspected, since increased dark uptake due to N-deficiency was found by Steemann-Nielsen and Al Kholy (1956). If the increased excretion of labeled material found by Fogg (1958) in an oligotrophic lake as compared to a eutrophic lake is due to deficiency rather than diminished illumination, it may be necessary to correct for excretron in oligotrophic waters. Certainly more research on the effects of deficiency on excretion should be done.

The effects of deficiency on photosynthesis and respiration have been reviewed by Pirson (1955). Photosynthesis at saturating intensities is inhibited by any mineral deficiency, but respiration generally remains constant or may increase. Thus, the P/R ratio decreases as deficiency progresses and correction for respiration will increase.

Ryther (1954b) first considered this decrease in the P/R ratio in comparing carbon-14 uptake with O_2 evolution. His results are shown in Figure 5, and indicate that, as nutrients become deficient, the carbon-14 data (uncorrected for respiration) are equivalent to net O_2 evolution. Incipient deficiency probably occurred from about the sixth to the tenth day and the last measurement probably represents photosynthesis by extremely deficient cells. One cannot tell from the description of this experiment exactly what element was deficient; presumably both nitrogen and phosphorus were deficient. Similar studies by Steemann-Nielsen and Al Kholy (1956) appear to refer to extreme deficiency and will be discussed below.

We have investigated the effects of nitrogen deficiency on carbon-14 measurements (Thomas, unpublished). Generally, with Dunaliella cells in the beginning stages of deficiency, uncorrected carbon-14 uptake was about 90% of net O_2 evolution, but also did not differ significantly from gross O_2 evolution. Although cell division ceased during incipient nitrogen deficiency, the culture continued to synthesize organic material, since both dry weight and organic carbon accumulated. K_2 values calculated from growth measurements did not differ significantly from those calculated from photosynthesis during incipient deficiency. During deficiency, dark uptake of carbon-14 increased, but this increase may be due to bacterial contamination in the aquarium culture rather than to deficiency per se.

Three comparisons of carbon-14 uptake and O_2 evolution during incipient phosphorus deficiency were also made. In one experiment carbon-14 uptake was much less than net O_2 evolution. In the other two comparisons the carbon-14 value was intermediate between net and gross O_2 evolution, and could not be distinguished from either O_2 measurement.

Carbon-14 Measurements with Extremely Nutrient-Deficient Algal Cells

Algal cultures that are extremely nutrient-deficient contain a minimum intracellular nutrient concentration and have ceased to grow. The P/R ratio in such cultures is generally less than 3, at least, and can be less than 1 if the culture is dying. Ryther (1954b) showed that when the P/R ratio was nearly 1.0, uncorrected carbon-14 uptake was quite comparable with net O_2 evolution (see Figure 5, measurement at 30 days). Gross O_2 production was several times net production. The results given for phosphorus and nitrogen deficient Chlorella cells by Steemann-Nielsen and Al Kholy (1956) indicate that the carbon-14 method yields results that are intermediate between gross and net O_2 evolution. Considering the relative errors of their measurements and the uncertainty of the photosynthetic quotient they used, it is difficult to determine which O_2 value is more comparable to carbon-14 uptake.

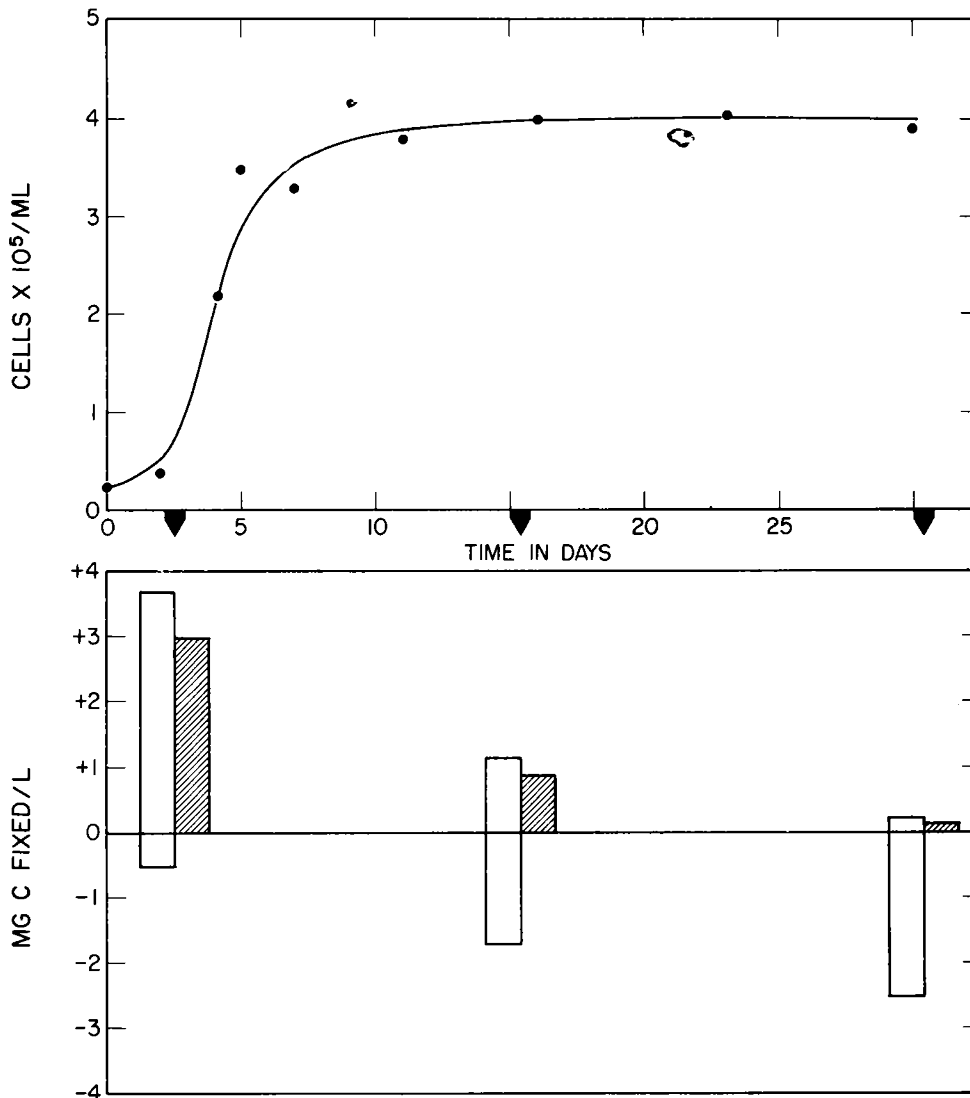

Figure 5— Photosynthesis measured by oxygen production (clear bars) and carbon-14 uptake (hatched bars) in a nutrient-deficient, pure culture of marine Chlamydomonas. Upper figure represents growth of culture determined by cell counts. (Reproduced from Ryther, 1954)

In our laboratory (Thomas, unpublished) we continued our nitrogen deficient Dunaliella cultures from incipient to extreme deficiency. The P/R ratio dropped to 2, and the intracellular nitrogen concentration reached a minimum level. In five comparisons of carbon-14 uptake (uncorrected for respiration) with O_2 production, the carbon-14 values were 80-100% of the net O_2 value, and 40-70% of the gross value. Uncorrected carbon-14 uptake was significantly greater than gross O_2 production. When one of these deficient cultures was continued even further, the P/R become less than 1. Under these very extreme conditions, carbon-14 uptake was still positive, but could not be compared with either O_2 measurement, due to analytical errors in the latter measurement that were nearly equivalent to respiratory and photosynthetic changes. Extreme phosphorus deficiency was not studied.

The above results refer only to nitrogen and phosphorus deficiency. Various enrichment experiments have indicated that purines and pyrimidines (Jones and Thomas, 1958) iron (Menzel and Ryther, 1961a), manganese (Harvey, 1947), and, for diatoms, silicon (Thomas, 1959) may limit phytoplankton production. At least, the addition of such substances to water samples can stimulate growth or production. Furthermore, the requirement of various phytoplankton species for organic growth factors (reviewed by Provasoli, 1958) suggests that such

factors may at times be deficient in the sea. At present we have no information on the effects of deficiencies of nutrients other than nitrogen and phosphorus on carbon-14 uptake.

Recovery From Nitrogen Deficiency

After extreme nitrogen deficiency was established, we added nitrate to Dunaliella cultures (Thomas, unpublished). In one experiment, after 21 hours of recovery, significant growth had occurred, cell nitrogen increased to the concentration characteristic of healthy, growing cells, and the P/R increased from 1.9 to 3.6. After recovery, carbon-14 uptake was intermediate between and equivalent to either net or gross O_2 production. The mean K_2 value for growth during recovery was 0.0324 hours^{-1}; that for photosynthesis after recovery was 0.0312 hours^{-1}. In another recovery experiment, similar changes in the P/R ratio and intracellular nitrogen level were observed. Again carbon-14 uptake was intermediate between, and equivalent to, either O_2 production measurement. Growth constants were not calculated for this experiment.

Nutrient Deficiency in the Sea

Evidence from enrichment experiments referred to above shows that nutrient deficiency occurs in the sea. Furthermore, nutrient concentrations in surface water may sometimes be below the concentration that limits the growth rate of phytoplankton cultures (Thomas, unpublished data, and others). However, data concerning the degree of deficiency (incipient or extreme) that exists in natural phytoplankton populations is very sparse.

Steemann-Nielsen and Al Kholy (1956) pointed out that under conditions of extreme deficiency, where the P/R ratio was less than 2, the algal population would not persist, and they suggested such extreme conditions would not occur (see also Strickland, 1960). The same authors showed that extreme nitrogen deficiency resulted in an increase of dark carbon-14 fixation to 37% of the light-saturated rate. However, in the North Atlantic and off Greenland, only a few determinations resulted in dark fixation greater than 10% of the light-saturated rate (Steemann-Nielsen, 1960). Thus, it seems doubtful that the population was extremely nitrogen deficient.

More convincing evidence against the occurrence of extreme nitrogen deficiency in the sea was obtained by Yentsch and Vaccaro (1958). They showed that the ratio of carotenoid pigments of chlorophyll-a increased in nitrogen-deficient cultures from a value of 0.22 to 0.40 for nitrogen-enriched cultures to 0.59 to 0.67 for the most deficient cultures. In Atlantic coastal waters ratios of 0.15 to 0.55 were observed, which suggested that natural populations were not as deficient as extremely deficient laboratory cultures. However, it should be noted that a few high ratios (>0.60) were reported from the same waters by Ketchum, et al. (1958a). These authors also showed that there was no clear relationship between these pigment ratios and the ratio of net to gross photosynthesis in Atlantic coastal waters.

In extremely nitrogen deficient Dunaliella cultures, the ratio of cell carbon to cell nitrogen increased to approximately 15 as compared with 5 to 7 in healthy growing cultures (Thomas, unpublished). The measurement of the C/N ratio of phytoplankton net hauls and more calculations of pigment ratios (from data already on hand) might provide additional insight into the intracellular nitrogen status of natural populations.

SUMMARY AND CONCLUSIONS

Of the four corrections that may be applied to raw carbon-14 data, three of them (for isotope effect, dark uptake, and excretion) are applicable for correcting carbon-14 data to both net or gross production. The theoretical correction for the isotope effect is about +5% and this value is found for long-term growth of algal cultures; the correction may be somewhat larger for photosynthesis periods of a few hours. To determine the isotope effect more precisely, direct comparisons of carbon-14 uptake with carbon assimilation would be needed for periods approximating those used in routine productivity measurements. A correction for dark uptake of tracer carbon is conveniently made by incubating darkened bottles with illuminated ones.

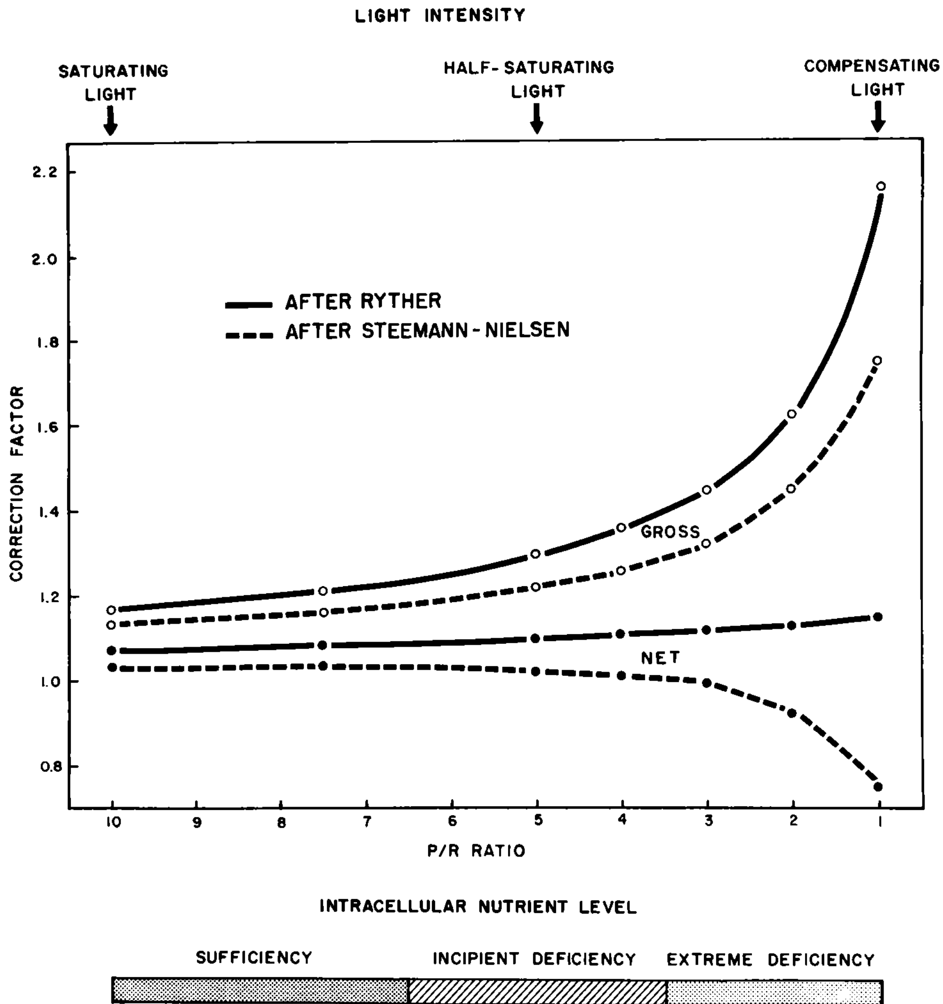

Figure 6— Factors by which raw carbon-14 data may be multiplied to obtain net (closed circles) or gross (open circles) photosynthesis at different P/R ratios. The factors are calculated assuming 100 percent intermixing of respiration with photosynthesis (solid lines— Ryther, 1956), or assuming 60 percent intermixing (dashed lines— Steemann-Nielsen, 1955). Also shown are light intensities and intracellular nutrient levels which would result in given P/R ratios.

Further investigation of factors affecting dark uptake may provide a powerful tool for measuring the nutritional status of natural populations. Investigations of excretion of previously labeled organic material and the rupture of algal cells during filtration have just begun. Present evidence indicates that this correction is just a few percent. Nutritional deficiency or subdued illumination may profoundly affect the amount of excretion, but much more research is needed on this problem.

The application of the fourth correction, for respiration (if a value for gross photosynthesis is desired), is dependent upon the degree of intermixing of respiration and photosynthesis and also upon the P/R ratio. The relationship between the P/R ratio and the overall correction factors to use to obtain either net or gross photosynthesis is summarized in Fig. 6. Correction factors assuming 100% intermixing of respiration (Ryther) and 60% (Steemann-Nielsen) are given. The isotope effect correction is included in the factor (assuming a +5% correction under all conditions); a correction factor for excretion is also included which is assumed to vary from +2% at a P/R ratio of 10 to +10% at a P/R ratio of 1. No correction is included for dark uptake; a separate dark bottle determination is assumed. As is indicated by Figure 6, if

one used a mean factor between Ryther's or Steemann-Nielsen's a calculation of either net or gross photosynthesis would scarcely be in error by an amount greater than experimental or sampling errors of the carbon-14 method, even down to a P/R ratio of 2. This range of P/R values covers nearly all conditions under which the bulk of phytoplankton photosynthesis is carried out. At P/R ratios less than 2, the uncertainties increase greatly.

Under conditions where the P/R ratio is high, the difference between net and gross photosynthesis is small. Carbon-14 results (uncorrected for respiration) agree with either net or gross O_2 evolution within experimental error, although carbon-14 values generally are closer to net O_2 values than to gross values. When both growth measurements and production measurements are carried out under similar conditions of illumination, growth rate constants (K_2) calculated from various growth measurements are in agreement with similar constants calculated from organic carbon and photosynthetic measurements.

The P/R ratio decreases with decreasing illumination. At subsaturating light intensities, carbon-14 uptake (uncorrected for respiration) is generally equivalent to or somewhat less than net O_2 evolution. At the compensation intensity, carbon-14 uptake is still positive. Incipient nutrient deficiency also decreases the P/R ratio and carbon-14 uptake is closest to net O_2 evolution, but also does not differ greatly from gross O_2 evolution. Growth and photosynthesis are quite comparable. Extreme deficiency greatly decreases the P/R ratio and carbon-14 uptake (uncorrected for respiration) is in good agreement with net O_2 evolution, but not with gross production.

Various means of establishing the degree of intracellular nutrient deficiency in natural populations have been considered. Pigment ratios, carbon/nitrogen ratios, and dark uptake measurements could be used. It would be of great interest to know if deficiencies occur in nature that are as extreme as those found in really deficient cultures.

ACKNOWLEDGEMENTS

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STATISTICAL AND SAMPLING PROBLEMS IN PRIMARY PRODUCTION

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I have been asked by our convener to discuss the statistical problems connected with the sampling of primary production. Thus I am not directly concerned with questions of meaning or validity of primary production as it is commonly measured. However, since my viewpoint is a slightly different one from the usual, it has seemed worthwhile to comment briefly on some apparent limitations of the estimation techniques in use, and to make some suggestions as to what lines of development may be most profitable in the future. While such a digression may seem irrelevant, I believe it is justified. I have misgivings as to whether many of our techniques do measure, even approximately, what they are generally believed to measure, and whether the objectives in taking these measurements are sufficiently clearly defined.

ERROR AND MICRODISTRIBUTION

Whenever we make a measurement of primary production I think we all realize that there is some uncertainty in this measurement, i.e. if we make the measurement again we will not get quite the same result. This uncertainty will include all the errors due to deficiencies in the technique we happen to be using, plus the errors due to the natural variability of the biological material. I am not primarily concerned with the question whether any given method overestimates or underestimates the true figure, though I will later refer to this second aspect, which we should call a "bias" rather than an error.

I will confine myself principally to the carbon-14 method, but most of the features I discuss will be applicable to other methods of direct measurement.

Errors may conveniently be divided into two categories: (1) The error of a single observation. (2) The error of a set of observations.

(1) The Error of a Single Observation

This might be called the error of technique, since it is concerned with the accuracy with which a single estimate from a single sample can be reproduced if the measurement is repeated a number of times. Unfortunately, in primary production, we are not in a position to repeat any one measurement because the technique itself destroys (or at least seriously alters) the sample. The best we can do is to take a large sample of water, homogenize it as well as possible by stirring, and then divide it into a number of subsamples. When compared with, say, a pure chemical compound, a natural biological sample cannot be regarded as completely homogeneous, so that the error obtained from measuring these subsamples will contain two components, one due to error of technique, and one due to the inherent biological variability of the material.

I have examined two sets of data of this type, one of my own, and one collected by Doty and Oguri (1958). In both cases, subsamples were drawn from a plastic bucket of sea water, thoroughly stirred. The results were in substantial agreement, both giving coefficients of variation of about 10%, which seems to be the minimum error which can be achieved by routine techniques in use at the University of Hawaii or Woods Hole Oceanographic Institution. Possibly this figure could be reduced by improved technique,* but, as will be seen below, 10% is a relatively small variation compared with that commonly encountered in nature, and it is doubtful whether any great elaboration in technique would be warranted on this account alone. Indeed it seems likely (even though this cannot be demonstrated experimentally) that the main component of variability is biological in origin. With resonable care, the physical part of the technique — volume measurement, filtration, and geiger counting — can be carried out with negligible error, but there is room for considerable variation in the size or photosynthetic capacity of individual cells, in their reaction to handling, and in their geometrical disposition on the filter. In practice, where statistical tests of significance or estimates are required, it will be desirable to set up the experiment to include an estimate of the error of a single observation.

To make the best use of our knowledge of variability, it is desirable to know something about the frequency distribution of the measurements. If we simplify the problem by assuming that the primary producers are randomly distributed particles, all of identical size and photosynthetic capacity, the distribution of measurements should be a Poisson series. The number of individuals will usually be fairly large — e.g., taking Skeletonema as an example — in a 125 ml bottle with a carbon-14 uptake equivalent to 0.1 ml $C/m^3/hr$ there will be about 40,000 cells. A Poisson series with such a large mean will be virtually identical with the normal distribution and will have a coefficient of variation of about 0.5%. As the number of organisms increases, the coefficient of variation will decrease. In actual practice, when I tried measuring the variability of production in a bacteria-free culture of Skeletonema, I found that even increasing the cell number to 10^6 per bottle did not reduce the variation below the usual 10% minimum. This still does not discriminate between biological and physical components of error, but it does suggest that the particulate nature of the producing organisms does not contribute substantially to the variability.

The actual frequency distribution of subsamples from a single sample of natural sea water does, in fact, approximate reasonably well to normal, and quite a few simple statistical tests can be made on this basis. However, since the variation is comparatively small (by biological standards), only gross departure from normality would be readily detected, and other distributions may be equally appropriate.

Since we are dealing with a distribution in which the standard deviation tends to remain a constant proportion of the mean, regardless of the size of the mean itself, it seems more appropriate to assume a log-normal distribution, i.e., that the logarithms of the estimates are normally distributed. We will see in the next section that this is much more convenient when we are dealing with field observations. For a normal distribution, the error is appropriately expressed as:-

$$m \pm s$$

(m = arithmetic mean, s = standard deviation)

and the coefficient of variation is:

$$V = 100 \frac{s}{m} \%$$

For a lognormal distribution, the error is better shown as:

$$m' \overset{\times}{\div} \text{antilog } s'$$

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*Dr. Charles R. Goldman (University of California, Davis, pers. comm) has found considerably less error in his freshwater lake investigations.

(m' = geometric mean, s' = standard deviation of logarithms of the measurements), and the coefficient of variation is:

$$V' = 100 \text{ (antilog } s'-1)\%$$

Provided V and V′ are fairly small, the difference between the two is not very great, though V′ is slightly larger, *e.g.*, for a *Skeletonema* culture I got:

$$V = 9.8$$
$$V' = 11.0$$

(2) The Error of a Set of Observations

When we are dealing with natural populations, there will be a further error component introduced by the disposition of the plankton organisms in space.

I have discussed the spatial distribution of plankton organisms in previous papers (e.g., Cassie, R. M., 1957, 1960, *in press*). It has been shown that plankters are seldom, if ever, randomly distributed in their natural environment. This fact has been known for some time (*e.g.* Hardy and Gunter, 1935; Barnes and Marshall, 1951) even if its implications have not always been fully recognized. Thus, instead of the Poisson (or random) condition where the variance (s^2 = standard deviation squared) of sample counts tends to equal the mean, it is usual to find that the variance appreciably exceeds the mean, or in mathematical terms that:

$$s^2 > m$$

This condition is best referred to as *overdispersion*,* and is defined by the inequality above. This statistical term is preferred (at least in the present context) to other synonyms:- contagion, schwarmbildung, patchiness, aggregation—since it is precise, yet at the same time does not contain any implication as to the mechanism generating a non-random distribution. Thus, an aggregation of plankton may exist merely as a result of environmental heterogenities without any social or contagious behaviour being involved. The reverse situation, *underdispersion* ($s^2 < m$) is theoretically possible, but seems to be sufficiently rare in plankton populations to be ignored.

The criterion ($s^2 \sim m$) is not available for primary production measurements, since individual organisms are not enumerated, nor is a simple Poisson distribution appropriate for a mixture of organisms of different sizes and kinds. Nevertheless, since production is a function of the quantity of phytoplankton, we will expect some measure of heterogeneity between samples taken in the field. The Poisson standard ($s^2 > m$) is replaced by the empirical standard ($V > 10\%$) and the term *overdispersion* must accordingly be replaced by the slightly less specific one, *heterogeneity*. Doty and Oguri (1958) took a series of primary production samples from a slowly moving vessel and found V to be about 25%, clearly an instance of heterogeneity in a relatively small spatial scale.

Intuitively, one might expect that there is some minimum sampling interval at which heterogeneity ceases to be apparent. In an effort to determine how small this interval may be, I quote the results of two experiments, one by the botany group at the University of Hawaii and one by myself, both based on essentially similar apparatus. My own consisted of a rack holding a row of 25 125 ml reagent bottles. The diameter of these bottles was 5 cm, so there were 25 samples taken at intervals of 5 cm. The whole rack was lowered into the water with the bottles inverted. Using a simple plankton-net closing mechanism, the whole apparatus was overturned so that all the bottles filled simultaneously. The bottles were then stoppered and passed through the usual carbon-14 routine, taking particular care to eliminate any variation in the treatment of the bottles.

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*Note the distinction between dispersion (of numbers) and dispersal (of things), two terms which are best kept separate in the present context.

I used this apparatus at several different stations on a cruise of the Crawford from Woods Hole, with the results shown in Fig. 1. The four stations were respectively in waters of the Gulf Stream, the Sargasso Sea, the Continental Slope and the Continental Shelf. The control consisted of 25 bottles filled, not from the sampler, but from a thoroughly stirred bottle of sea water. Two parameters are plotted. The standard deviation of each set is s, and R^2 is the square of the serial correlation (or autocorrelation) coefficient of the samples taken in the order in which they were placed on the rack. Both parameters are calculated from the logarithms rather than the raw counts, for reasons which will become evident below. I do not

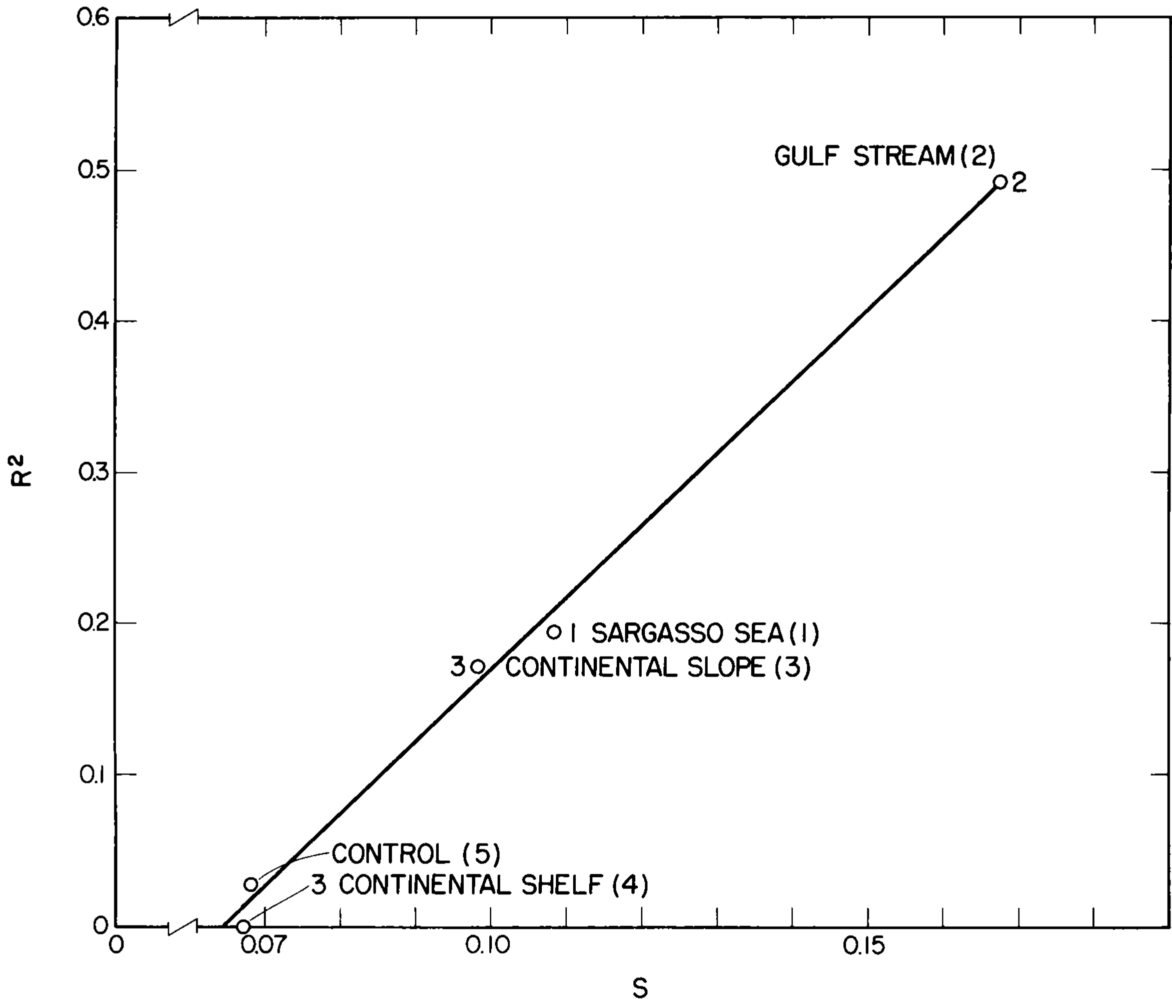

Figure 1. Serial correlation squared (R^2) as a function of the standard deviation (S) of plankton sample counts at four stations.

think there is any particular significance in the properties of the particular localities, except that they do represent a range of different oceanic conditions. Nor do I think that the linearity of the regression line is very important. The main point of interest is that the greater the variability of the set, the greater the serial correlation. All except the bottom two correlations are significant at the 5% level, indicating that production in any one sample is partly related to that of adjacent samples and therefore cannot be entirely random. This is so despite the fact that the samples were only 5 cm apart, and the whole apparatus was only about 4 ft (1.25 meters) long. Although it is not immediately evident, this test includes, in effect, the error of a single observation; since correlation can only be detected when it is sufficiently high to be apparent above the "noise level" produced by the error of individual measurements.

Serial correlation is not always a very sensitive test for non-randomness, and I was perhaps lucky to obtain reasonably conclusive results. The Hawaii people tackled the problem in

a different way. They used larger bottles with a spacing of 15 cm and split each one into two subsamples. It was then possible to use the differences between pairs of subsamples as a measure of error, and then by analysis of variance to show that the differences between different bottles were significantly greater ($P < 0.01$) than those within a single bottle. It is interesting to note that their data do not show any serial correlation; which suggests that the bottles were too far apart for any two of them to come within one aggregation of phytoplankton. I have not got nearly enough data to be certain of this, but it would appear that the largest parcel of sea water which can be considered as approaching homogeneity, is rather less than 5 cm in diameter.

The mathematical distribution of this kind of error becomes of considerable importance for any quantitative ecological work because we can scarcely hope to sample the whole ocean 5 cm at a time. Once again, we start from the assumption that primary production is at least in part a function of the numbers of producers. Fig. 2 shows, in a simplified graphical form, a mathematical model (Cassie, in press) developed on the basis of known distributions of plankton counts. Along the bottom, a series of normal distributions represents a complex of physical and chemical properties of the sea environment (temperature, salinity, oxygen, etc.) all properties being variable, and their variation normally distributed. Each of these properties contributes to controlling the distribution of the plankton, and also the sum of all components is normally distributed. The reaction of organisms to a changing physical property is usually an exponential one:

$$Y = e^{(a+bX)}$$

(Y = number of plankters, X = value of the physical variate, with a and b constant). This equation is represented by the curve between the X and Y coordinates on the diagram. Using this curve it is a simple matter to transform the normal distribution to the log-normal representing the "expected" frequency distribution of the plankton. This, however, does not complete the model, since we have to take into account the role of chance in controlling the movement of individuals. This is done by constructing an infinite series of Poisson distributions (represented by four in the figure)—one at every point along the log-normal curve and taking their sum, which gives the distribution on the top right. The arithmetic involved in handling this distribution is very laborious but fortunately, provided the mean number of organisms per sample is large (say 50 or more), we can ignore the random component and treat the distribution as a simple log-normal. I have already postulated that a primary production measurement is a function of a relatively large number of phytoplankters, usually several thousand per sample, so that we might suspect that the log-normal model will be appropriate for handling the data. The conversion from plankton to primary production is not 100%, because we are not dealing with a homogeneous collection of producing units. In fact, the producers come in all shapes and sizes and physiological conditions. I have not tried to develop an exact model for this variability component, but it seems that the distribution generated is as likely to take the log-normal as any other form.*

In my multiple sampler data, 3 out of 4 of the sets fitted the log-normal perfectly, the third not quite so well, but the discrepancy was relatively slight.

What does all this mean from the practical point of view? Fortunately the log-normal distribution is very easy to handle statistically. One simply converts the data to logarithms and treats them as normally distributed. Since most modern statistical theory is based on the normal distribution, this immediately opens the way to a whole gamut of statistical techniques such as regression and correlation, analysis of variance and covariance and discriminant functions. In a recent paper (Cassie, in press) I have described a method based on log-normal probability paper by which a collection of regional plankton counts (or, for present purposes, productivity measurements) may be dissected into the component populations. This technique may be a useful tool in discriminating between biologically different water masses.

*Those familiar with the current statistical literature will immediately think of the negative binomial distribution. For large samples the distinction between this and the log-normal is such a fine one, it need hardly concern us.

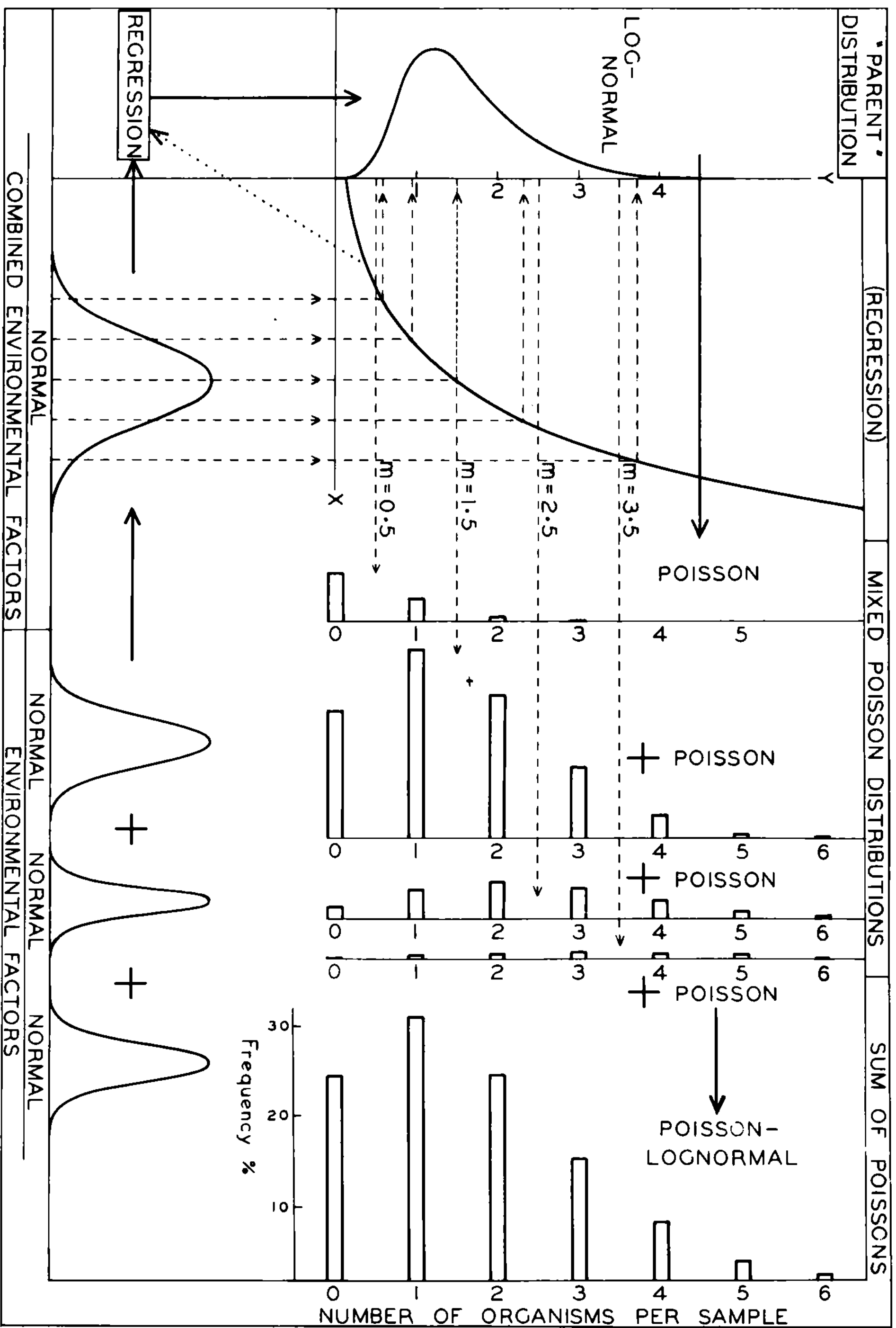

Figure 2. Mathematical model of known distributions of plankton counts.

I do not want to give the idea that, because a relatively satisfactory statistical procedure is within reach, all our primary production troubles are over. I will present just one set of data which reflects on another problem—are we measuring what we think we are measuring? Fig. 3 represents a continuous record of the dissolved oxygen content of a bacteria-free culture of Skeletonema. This was enclosed in a reagent bottle and incubated more or less in the normal light-dark bottle manner, except that the contents of the bottle were stirred with a magnetic stirrer and the dissolved oxygen content was continuously monitored with a polarographic electrode. At 1600 foot candles (f.c.) there was an increase in oxygen, representing a positive net photosynthesis. In the dark, oxygen decreased—representing respiration. At 600 f.c. the rate of oxygen consumption actually increased over the dark rate, so that if we add respiration algebraically to net photosynthesis, we get a negative gross photosynthesis, which is nonsense. Apparently, in this particular situation, respiration is greater in the light than in the dark, which contradicts one of the fundamental assumptions of the light-dark bottle oxygen technique. It also raises some question as to the validity of the dark-bottle correction

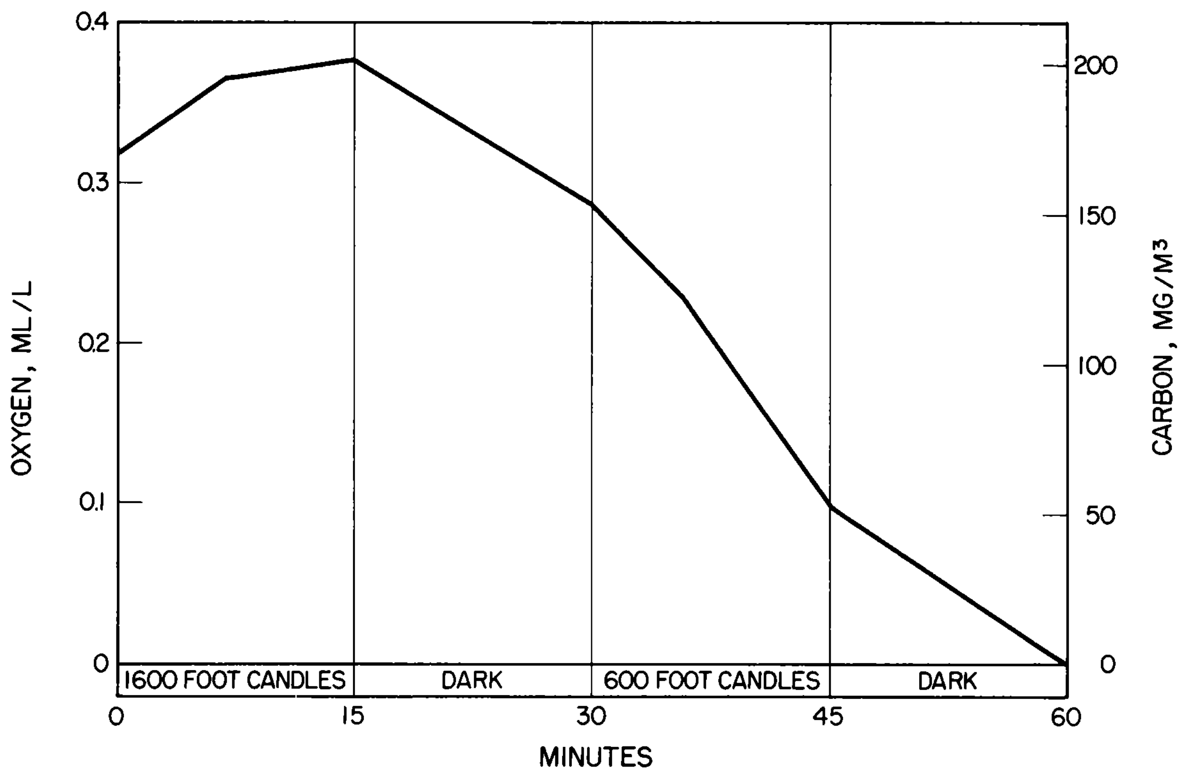

Figure 3. A continuous record of the dissolved oxygen content of a bacteria-free culture of Skeletonema (23×10^6 cells/liter).

for carbon-14 estimates. Although net production at 600 f.c. was negative, the culture from which the sample was taken continued to grow at a light intensity of 300 f.c.—another contradiction. It seems that the mere fact of removing the sample from the culture flask to a stoppered bottle had materially changed its behaviour. This makes me wonder how well a bottle experiment represents what is going on in the sea. I do not think it makes much difference whether the bottle is on the deck of the ship or lowered back into the sea. In both instances the conditions have been substantially changed by enclosing the sample in a bottle.

In a further experiment, I followed virtually the same procedure, except that the culture was inoculated with carbon-14, thus enabling a second independent estimate of production to be made. Despite the negative oxygen production, a substantial amount of carbon-14 was retained, even after subtracting the uptake in a dark-bottle sample inoculated at the same time.

This is at variance with Ryther's (1954b and 1956b) hypothesis that the carbon-14 technique measures net production. Ryther's statement may indeed be true under a certain range of circumstances, but it is evident even from his own Fig. 1 (1956b) that it can only apply above the compensation level of illumination. It would be more realistic to say that, when photosynthesis exceeds respiration, carbon-14 uptake is approximately equivalent to oxygen evolved. Possibly this equality is the result of compensating biases rather than any fundamental equivalence of the two measurements to net production.

The experiments I have quoted were repeated several times, and the results found to be reproducible. Probably all the phenomena revealed are familiar to others in the primary production field, though I am not aware of any published work in which serious attention has been drawn to them. While it is generally realised that productivity measurements are only approximations, some of the biases involved are of too gross a nature to be lightly dismissed.

DEVELOPMENTS FOR THE FUTURE

How should we develop our production ecology in the future? I have already stressed the need for reassessment of techniques. A true "in situ" method of measurement, free from bias resulting from artificial enclosure of the sample, would be a "break through" of considerable significance, but does not seem to be in sight at present. On the other hand, even a biased estimate can be useful if it can be related clearly to the end-point of the enquiry. Production, after all, is a fisheries (or an agricultural) concept and implies that some crop is removed for another purpose, otherwise the integrated production will be zero. If, for example, we are interested in predicting fisheries potential, it matters little whether our estimate of primary production is biased or unbiased, or even if it really is primary production, provided it can be related to the ultimate prediction.

Two main lines of investigation seem to warrant further development. The two, which may be labelled for convenience the field and the laboratory approach respectively, are complementary and neither can develop indefinitely without some aid from the other. The first depends more upon field observation and empirical deduction, the second upon a more fundamental biological approach.

(1) The Field Approach

There has been a tendency to regard productivity and other energy budget concepts as being rather a different field of endeavour from the older type of ecology which looks at animals and plants as species, enumerates them and tries to account for their behaviour in relation to their environment. On the other hand, this type of information is still being collected on a large scale, and techniques for handling it are gradually being brought to a greater level of precision. I feel that primary production should be regarded as another member of this family of ecological variates, and that we should be developing means of multivariate analysis by which the relationship between them can be expressed mathematically, on a complex rather than a simple scale. Before the days of electronic computers we were forced merely to skim the cream off our data, pick out pairs of variates which were obviously correlated, and forget the rest. Now we can do better than this. A start on the multivariate type of plankton ecology, has, in fact, been made in various laboratories.

Some of the earliest work of this kind is presented in a series of papers by Riley and various collaborators. For example, Riley (1946) developed empirical multiple regression equations relating phytoplankton population to temperature, phosphate, nitrate and total zooplankton population. More recently, Holmes (1958a) has used the regression approach, expressing zooplankton volume as a function of primary production and chlorophyll-a. Steele (1956, etc.) has further developed the theoretical approach. I have expressed the numerical abundance of individual species of plankton in terms of temperature, salinity, and other plankton species (Cassie, R. M., 1960), while Moore (Moore and Corwin, 1956; Moore and Bauer, 1960) has made a similar analysis of the vertical distribution of plankton as related to temperature, pressure and light intensity. Williamson (1960) has processed data from the Hardy

plankton recorder by constructing species x species correlation matrices. From these, principal components of variation in the ecological complex may be extracted and in turn correlated with environmental factors.

The empirical treatment of data by correlation and allied techniques has, of course, certain limitations. It cannot differentiate between cause and effect, nor can it demonstrate with certainty whether the primary causal factors have even been measured. Nevertheless, the application of suitable mathematical models can, in the hands of a critical investigator, be a powerful tool which will extract maximum information from multivariate data, showing which measurements are likely to be of greatest significance, and giving some clues as to the causal mechanisms involved.

(2) The Laboratory Approach

As one who has devoted most of his time to the first approach, I will not attempt to review the advances which have been made in this field, or to point too specifically at problems. I do feel that there is at present a gap between the empirical primary production experimenter and the biochemist or plant physiologist who is more fimiliar with the detailed mechanism of photosynthesis.

We know, for example, that photosynthesis is, quantitatively, a function of chlorophyll and light. Ryther and Yentsch (1957) have suggested that in order to estimate gross production at light saturation, the weight of chlorophyll-a may be multiplied by the approximate assimilation quotient (AQ), 3.7. No great precision is claimed for this figure, and within the set of circumstances for which it was derived, it produces an acceptable estimate, perhaps just as acceptable as an oxygen or carbon-14 determination. On the other hand, it is doubtful whether the same quotient will be universally applicable. Even within the area in which the technique has been applied (Ryther and Yentsch, 1958), the best estimate of AQ varies from 2.5 to 4.1 for four different cruises. An analysis of variance shows that these are not mere chance variations, being significant at the 1% level of confidence.

These discrepancies undoubtedly arise because light and chlorophyll-a are not the only two relevant factors. They may perhaps be the two principal single elements, but we still have not begun to take into account quantitatively the full complexity of the metabolic paths involved in photosynthesis and respiration. It is in this region that we will have to call in the biochemist before we have made too many grand oversimplifications.

Acknowledgments

The presentation of this paper has been made possible by a grant from the U. S. Atomic Energy Commission. Thanks are due to our convener, Dr. Maxwell S. Doty for his encouragement in the presentation of my views and for the use of unpublished data. Much of my knowledge of current trends in primary production research, I owe to Dr. John H. Ryther, in whose laboratory I have recently been priviledged to work for seven months.

SIGNIFICANCE OF THE VALUES OBTAINED BY PRIMARY PRODUCTION MEASUREMENTS

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INTRODUCTION

There are, I suggest, five main questions that students of marine primary productivity need to ask themselves about any sea area. What phytoplankton species are present; how much plant material is present and what is its composition; how fast is it growing; why has it the observed composition (that is to say why are some species growing rapidly compared with others) and, finally, by what organisms are the plant cells being eaten and how effective is their utilization in the overall marine food cycle? The significance of any value obtained by productivity measurement must be judged on the basis of how many of the above questions are answered, or partly answered, as a result of the measurement.

Few if any of the basic problems encountered in primary productivity research are peculiar to the Pacific area as such. They are however, as important to those of us working on the waters of this ocean as to anyone else and it may not be out of place at the conclusion of this symposium to discuss briefly "the significance of values obtained" by present day techniques.

It seems to me that time has now come for a complete re-appraisal of the aims and purposes of productivity research. The "pioneer" era of the last half century is now at an end. Modern techniques and increasing numbers of personnel have made possible a great increase in the number and kinds of measurements that can be made. It behoves us, therefore, to consider most carefully the significance of the results we are getting, and make sure that what meager efforts we can muster (meager when set against the magnitude of the tasks that face us) are not wasted.

STATISTICAL SIGNIFICANCE

There is little to be said on this aspect of "significance" that has not been stressed already, either in this symposium or elsewhere.

The standard deviation of a method applied to a uniform water sample should be known, at least approximately, by every worker. Suggested values for the precision of most techniques and their limits of sensitivity have been published by Strickland and Parsons (1960) and it is not difficult for any analyst to derive similar data for his own methods. It is now mandatory that workers in all fields of marine research express their results in some statistically meaningful manner (Strickland, 1958a).

Of course, in most cases, the precision of sampling is much less than that of the chemical or physical measurements made on the sample taken from the ocean. We have already had an excellent account of this in the present symposium. The observations made by Cassie (1959a) of the variations in the natural distribution of a Coscinodiscus over distances of less than a foot might make one despair of ever obtaining a meaningful sample of a natural population. However, the suitability of any sampling procedure cannot be divorced from considerations of the use to which results will be put. The subject has been reviewed by Strickland (1960) and there seems little doubt that, for rough estimates of total standing crop, the technique of pumping sea water through a plastic pump and hose assembly is quite adequate.

One might go further and suggest that for many purposes semi-quantitative estimates of standing crop might suffice, providing such estimates were made frequently and could be obtained over several thousand square miles of sea during a very short period. I am thinking, in particular, of monitoring the onset and location of phytoplankton blooms in coastal waters. Clearly only aircraft could be used for such a purpose. Aircraft will have increasing importance for "surface" oceanography and we should not lose sight of their potential in primary productivity work. Strickland (1961) has outlined a method whereby the back-scattered radiation from the sea, measured by a suitable combination of photocells, might be used to detect variations in the concentration of particulate matter. The method is now under trial and shows promise in coastal waters although its use is not expected to be practical over the clearer areas of the open ocean.

Heterogeneity of population causes a much more serious sampling problem when we wish to measure photosynthetic rates. The use of sampling bottles then seems essential (ref. Strickland, 1960) and the amount of work required for a really representative sampling program becomes formidable. In situ "incubation" of the sampled water is the nearest approach to a satisfactory technique (ref. Strickland, 1960) but this is rarely possible in the ocean and some form of constant light incubator must be used. We then face the serious problem that the photosynthetic characteristics of a plant population vary with depth whenever the euphotic zone is deeper than a well-established thermocline or halocline (ref. e.g. Ryther and Menzel, 1959; Steemann-Nielsen and Hansen, 1959b). "Light" and "shade" cells (even of the same species of phytoplankter) can exist either side of a density discontinuity that has persisted for more than a day or two. Recently, Ryther and Hulburt (1960), have made the startling discovery that there can be a stratification of phytoplankton species even in water which would be considered completely mixed by ordinary oceanographic criteria.

Finally, of course, one must be on guard against errors due to the diurnal variation of photosynthetic potential first recognized by Doty and Oguri (1957) in the sub-tropical Pacific. Fortunately for those of us working in sub-arctic regions, there is little effect at latitudes greater than about 45° (Doty, 1959b).

CONVERSION OF MEASURED VALUES TO ABSOLUTE VALUES

I would like to discuss this problem in some detail as it is pertinent to the whole question of the significance of primary productivity measurements. What we really need to measure in productivity research is the absolute amount of plant material in the sea and the rate at which it is increasing or decreasing. Such an ideal is never achieved.

(a) Cell counts

Microscopic examination permits the nearest approach to an absolute evaluation of the standing crop of plant cells. Cell numbers have been, and still are, quoted by numerous workers, generally as a "by-product" of taxonomic studies. The method is very time-consuming but the results are worthwhile if they are used over a period of many days in a limited sea area to illustrate the succession and spatial heterogeneity of various species. Unfortunately this is all too rarely done and, when not done, cell enumerations seem to me to be nearly pointless.

Cell counts can easily be made meaningful, however, if first converted to cell volumes by using even the roughest of conversion factors. Lists of such factors have been quoted (ref.

e.g. Laevastu, 1957; Paasche, 1960b) but the number of species in the phytoplankton is much too large for any existing computation to be of wide applicability. It is relatively a simple matter, and little extra work for the microscopist, to estimate the cell volumes of the species he is counting as he counts them, so species lists are really not essential. The volume of an awkwardly shaped cell can be estimated by using a plasticene model, made to scale, measuring the water displacement of the model in a measuring cyclinder. As a refinement, the vacuole volume of the larger diatoms should be subtracted from the total volume of the cell (Banse, 1956). Anyone who has bothered to make the conversion of cell numbers to cell volumes in a mixed population will be left in no doubt of the misleading view of the composition of the standing crop that is obtained from cell numbers alone (ref. e.g. McAllister, et al, 1961, Paasche, 1960a and b). In a recent paper Paasche (1960b) has shown that the total surface area of the phytoplankton may be a better measure of its photosynthetic potential than the total cell volume.

(b) Chemical composition

Strickland (1960) and others, have suggested that the best single measure of the standing crop of phytoplankton is the amount of plant carbon in a seawater sample. For other purposes a knowledge of the plant protein, carbohydrate or lipid may be more desirable.

Recently, methods for the determination of these quantities in the particulate matter in sea water have been published (Parsons and Strickland, 1959; Strickland and Parsons, 1960) but these methods do not differentiate between the plant cells in a sample of water and the animals or detritus of a similar particle size. The principal problem in standing crop measurement is now the separation of living plant material from detritus and animal matter. Separations by settling (or floating), as achieved by Anderson (1959) with benthic animals and detritus, is out of the question with the wide range of particle sizes found in the microplankton. The most hopeful lead I have seen comes from mineralogy! The commercial separation of many minerals from each other and from unwanted rock depends on treating a fine slurry of rock and mineral in water with chemicals that modify the surface properties of one or other constituent and facilitate the attachment of this constituent to air bubbles rising through the slurry. In this way particles are swept to the surface and can be scraped off attached to the bubbles of a surface foam, leaving smaller particles and lighter material still in the body of the liquid. Recently Gaudin et al (1960) have succeeded in using such a technique for the pilot-scale separation of bacteria spores, cells and debris from each other. By adding suitable chemicals, such as amines and fatty acids, quite good separations were possible. We should be able to devise some similar treatment to give the surface of a living plant cell (oxygen rich) a different "wetability" from any animal and detrital surfaces in the same sample.

At present, however, the only rapid measure of the plant material in a seawater sample is via the characteristic plant pigments, notably chlorophyll-a. To convert the latter values to the true amount of plant carbon, etc. requires the use of conversion factors. If the correct factor is known, then the total organic particulate matter, which may be determined by direct chemical analysis, can be correctly apportioned between plant and detrital material. This has already been attempted by Gillbricht (1952) and Banse (1956) and, in full detail, by McAllister et al, (1960).

Strickland (1960) reviewed the literature and concluded that the factor for converting chlorophyll-a to plant carbon is so variable that no one value has general applicability. Any figure between about 20 and 70 is possible for mixed natural populations. Since then, work at the Nanaimo laboratories of the Fisheries Research Board of Canada, using cultures of open ocean and coastal populations, has produced more factors for converting chlorophyll a to carbon, carbohydrate, protein and lipid (see McAllister et al, 1960 and 1961). Parsons et al (1961) have extended this work to a dozen different unialgal cultures of marine phytoplankters, grown at moderate light intensity in the presence of excess mutrients. Much more work is still required, however, as factors depend not only on the nature of the algae but on the conditions of light, temperature, and nutrition. In particular, nitrogen deficiency, persisting long enough for cells to undergo two or more divisions, greatly increases the amount of carbohydrate and fat relative to the amount of protein. Eventually there is a marked de-

crease in the quantity of chlorophyll in each plant cell, and all chlorophyll conversion factors increase. Furthermore, changes of cell pigment content with time of day may be appreciable even in sub-arctic coastal waters (Yentsch and Ryther, 1957; Yentsch and Scagel, 1958). Some idea of the nutrient level of the water and the nature of the main plant species present will have to be known before we can estimate conversion factors with any degree of certainty.

(c) Plant pigments

There has been much speculation as to the significance of pigment composition and pigment ratios (quantities that can be determined relatively easily) in productivity work, the hope being that this data is related to the composition of cells or to their photosynthetic potential. The position is far from satisfactory and it seems to me we may be tempted to make sweeping generalizations on matters which are too complex for any such generalizations to be justified.

The pigment content of unicellular algae is certainly very sensitive to growth conditions. (Twenty years ago Haskin (1941) reported the formation of two new xanthophylls in Chlorella cells simply as a result of nutrient deficiencies.) For example, chlorophyll-c was undetected by Dales (1960) in his study of the Chrysophyceae. We have found at Nanaimo that although this pigment is virtually absent in vigorously growing cells of Monochrysis lutheri it does occur in old and brightly illuminated cultures and is present in appreciable amounts in Coccolithus huxleyi. Similarly Allen et al, (1960b) have reported diatoxanthin but no diadinoxanthin present in the Chrysophyseae. Dales (1960) found just the reverse. Again, Goodwin (1957) generalized about the xanthophyll components of the Cyanophyta based mainly on the analysis of certain Nostocales but his observations are at complete variance with the results obtained by Parsons (1961) on Agmenellum quadruplicatum and a Synechococcus sp. in the order Chroococcales. Yentsch and Vaccaro (1958) found a linear relationship between cell nitrogen and the carotenoid to chlorophyll ratio in several algae. Although Haskin (1941) reported that the total pigment content of Chlorella decreased drastically in nitrogen starved cells, he noted that the ratio of carotenoid to chlorophyll was much less variable. McAllister et al, (1961) in the "sea bag" experiment found the ratio almost unchanged in plants that had lived for six days in nitrate depleted water.

However, certain facts do appear to be generally agreed upon. The carotenoid to chlorophyll ratio increases at high light intensity and at low temperature (ref. e.g. Yentsch and Scagel, 1958; Halldal, 1958). We have witnessed at Nanaimo a most striking increase of the ratio (some three-fold) when the temperature of a culture of Monochrysis lutheri was lowered by 8°C. Most interesting of all is the chlorophyll-c to chlorophyll-a ratio in coastal and oceanic populations. This ratio was greater than unity in natural populations and in cultures grown in water taken at 50° N and 145° W (McAllister, et al, 1960) whereas in British Columbia coastal waters (in nature and in cultures) the ratio rarely exceeds 0.6 (Parsons, 1960; McAllister, et al, 1961). In most of the unialgal cultures grown at Nanaimo, which are "coastal" in origin but which include species from all the main classes of the marine planktonic algae, the ratio is less than about 0.6 (Parsons, 1961). Other workers have confirmed these observations (e.g. Currie, 1958; Humphrey, 1960). The difference between coastal and open ocean results must be related to the species found in the two environments. This does not explain matters, however, and the solution of this problem as well as the exact significance of the results remains a challenge. It is interesting to note that whenever the measured ratio has approached unity in the sea off the British Columbia coast the crop density has been comparatively low. We have found this to occur both in summer and in winter (Parsons, 1960) and the effect does not seem to be all attributable to an analytical artifact. Work at Nanaimo, using cultures and also making observations at sea, has convinced us that a low carotenoid to chlorophyll ratio is characteristic of "detrital" plant material.

Finally, a word of warning should be sounded concerning the "Richards" method for phytoplankton pigment analysis. The adoption of this method by marine laboratories all over the world was inevitable and has greatly improved the general standards of pigment estimation. The use of 90% acetone, however, does have limitation as the cells of many species are not extracted or the pigments may be incompletely extracted. Furthermore it is almost impossible, without microscopy, to be sure which, if any, of the samples from a natural population are in-

completely leached. The formula used by Richards for chlorophyll-a estimation has been criticized (see Odum et al, 1959). The formulae for calculating chlorophyll-c and carotenoid concentrations needs extensive revision. Work at Nanaimo (to be published soon) has shown that the specific extinction coefficients of fucoxanthin and peridinin, the two most common marine carotenoids, are only about one half of that assumed by Richards. We have also estimated the specific extinction coefficient of chlorophyll-c. The MSPU for this pigment turns out to be considerably less than one milligram.

All these criticisms, of course, do not detract from the general usefulness of the procedure, provided that we do not endeavour to interpret results too precisely or to use the method in circumstances for which it was never intended. For many purposes, the ratio of absorbancy at 4300A and 6650A can be a useful property, especially for indicating waters rich in dinoflagellates (ref. e.g. Margalef, 1960).

In particular, one should always be on guard for the presence of phycobilin pigments. These may or may not extract into 90% acetone but, when they are extracted, results using Richard's formulae can be completely misleading (ref. Strickland and Parsons, 1960).

The time has come for a complete re-investigation of marine plant pigment methods, using a solvent or mixture of solvents with greater extracting power than 90% acetone and determining the exact extinction coefficients of each of the main plant pigments in the new solvent. A separate technique, directed specifically towards the phycobilins, would be useful. It now appears that these latter pigments may characterize the Cryptophyceae as well as the Myxophyceae (see Allen et al, 1959, and other authors). The presence of the Myxophyceae in low concentrations may be more general than we have realized and have considerable importance because of the nitrogen fixing powers possessed by many species in this division (Allen, 1959).

(d) Photosynthetic rates

So much has been said about the significance of photosynthetic rate measurements that there seems little point in adding to it here. Strickland (1960) has reviewed much of the subject up to 1958-59 and little has appeared in the literature since then that greatly changes the situation. Whatever may be said in criticizing the radio-carbon method it remains the only technique by which any sort of a result can be obtained in the open ocean, and we should be thankful! It is not often appreciated that the possible variations in photosynthetic quotients are so great that the interpretation of results obtained by the oxygen "light and dark bottle" method is also far from simple (ref. e.g. McAllister et al, 1961).

The most serious fault that I have to find with quantitative photosynthetic rate experiments is the reluctance of workers to state the spectral energy distribution of their light sources or to measure light intensities in absolute and reproducible energy units. Until this is done, most of the results appearing in the literature will have no quantitative application and, indeed, it is unlikely that results on the same populations will be reproducible from one institution to another. At Nanaimo we are standardizing on a spectral distribution approximating that of sunlight that has penetrated a few metres of fairly clear coastal water. This can be obtained by using overrun tungsten lamps and a simple chemical filter. All light intensities are recorded as cals/cm^2/min of radiant energy by means of a thermopile bolometer.

I would like to suggest that a most worthwhile long-term program in marine photosynthetic rate work would be the compilation of a "handbook" of growth constants for the more common species of phytoplankton or representative species from each of the main orders. At any instant the growth of a population (p) of unicellular organisms can be expressed by:

$$\frac{dp}{dt} = k.p$$

where the constant k is a function of temperature, salinity, light and nutrient environment. Although k depends upon the prehistory of cells and is a complex function of many variables, I suggest that the tabulation of k values for any species may not be as impossible a task as might be supposed. If we concentrate on conditions likely to be encountered in a given sea area and use modern techniques of factorial analysis (e.g. Davis, 1956) then a growth constant tabu-

lation for many species could be obtained in the foreseeable future. With such information, and the use of sophisticated methods of water analysis, it would be possible to predict the observed succession of algal species in the sea. This is one of the main aims of primary productivity kinetics and of great practical value.

When estimating the total fixation of carbon by photosynthesis it should be remembered that many of the phytoplankters are capable of heterotrophism, that is to say they may be accumulating cell substance directly from dissolved organic matter in the surrounding water. The ability to grow heterotrophically has been reported for species from most of the main divisions of the algae, although only studied extensively in the Chlorophyta. Photosynthetic and heterotrophic growth processes may be additive in the same plant cell. There can be little doubt that in nature certain diatoms, coccolithophores and microflagellates, assimilate carbon heterothrophically and our normal methods of estimating cell increase will give low results (Rodhe, 1955; Bernard, 1948 and 1958; Smayda, 1958; Wood, 1956 and 1959; Lewin and Lewin, 1960). McAllister et al, (1961) in the "sea bag" experiment detected what was almost certainly heterotrophic growth by a mixed pelagic population of Thalassiosira and Skeletonema kept at very low light intensities.

SIGNIFICANCE OF PRIMARY PRODUCTION IN THE MARINE FOOD CHAIN

We come now to what is probably the most significant question of all in primary productivity research; how well, and by what organism, are the plant cells being utilized in the food chain? To quote from Marshall and Orr (1958a) "Little is known of the chemical composition of phytoplankton and its nutritive value. A knowledge of these and their seasonal cycle in the sea in relation to the Copepod population is one of the most pressing problems in the study of marine productivity".

Let us assume a far off and ideal time when we may know what species are present in a sea area and can measure their composition and rate of increase. This information will still be of little use to marine ecologists, and hence to the fishing-interests who sponsor most of our researches, unless we also know how good the plant material is as a feed for secondary producers. The responsibility for this phase of any unified program of marine research should properly belong to those of our biology colleagues who are concerned with higher links in the food chain. However, with a few notable exceptions, I have seen very little lead from this direction. Information on the subject is widely scattered through the literature and I can only summarize here some of the experiments that have come to my attention and mention a few of the results obtained in my own laboratory.

For the correct assessment of the food value of any plant crop we should know its "proximate" analysis for the major metabolites, carbohydrate, protein and fat and for ash, as is done in terrestial agricultural practice. Furthermore, a breakdown of the carbohydrate into insoluble fibrous material such as cellulose (called here "crude fibre") and the soluble sugars would be helpful. An assay of the carbohydrates and proteins in terms of component sugar and amino acid units and of the lipids in terms of their fatty acids should be attempted. Some estimate of the composition and "toughness" of the cell wall of each species (marine membrane chemistry) is desirable and finally the cell protoplasm should be assayed for its content of growth factors such as the B-vitamines.

All this work is properly the task of those of us concerned with the ultimate measurement of primary productivity but "the proof of the pudding is in the eating," as it were, and the final test of whether a given animal will ingest and digest a plant cell and how well it will profit thereby can only be made by feeding trials with the animal itself. This is properly the responsibility of those studying secondary protection.

There is, without doubt, an enormous amount of work required by all of us before the above program, which would now be considered by some to be extremely ambitious but which is only a minimum dictated by common sense, could be completed even in its elementary stages. However, the time has come when such work must be undertaken at an increasing tempo. We must have this data if we are to progress from the stage of making ad hoc multiple correlations to a clear understanding of what is going on in the sea; an understanding which alone can enable sure predictions to be attempted.

(a) Composition of algae

Strickland (1960) has already pointed out the regrettable shortage of values for the major metabolites in the marine planktonic algae. The fresh water Chlorophyta, by contrast, have now had a fairly thorough preliminary survey, and show a surprisingly good spectrum of amino acids, sugars and lipids (ref. e.g. Fogg, 1953; Hundley et al, 1956; Strickland, 1960; Schükerk, 1960; Williams and MacMillan, 1961). Krey (1958b) has recently reported some analytical work on diatoms, ceratia and mixed plankton, and Rho (1959) gives a gratifying full analysis of Nitzschia closterium. The lipids of diatoms have had their fair share of investigation (Lovern, 1936; Clark and Mazur, 1941) but there has been little work on sugars and amino acids, save for the very detailed analysis by Barashkov (1956) of the carbohydrates of diatoms, and by Low (1955) of the amino acids. The proximate metabolite analyses for a mixed "coastal" population (mainly diatom) has been given by McAllister et al, (1961) in the "sea bag" experiment.

As far as I know, the most thorough preliminary survey of the chemical composition of individual marine phytoplankters yet attempted has just been completed at Nanaimo by Parsons et al, (1961). The amounts of carbon, carbohydrate, "crude fibre," protein, lipid, silicon, phosphorus, nitrogen, ash and plant pigments have been determined on one or two marine species from each of the Chlorophyceae, Chrysophyceae, Bacillariophyceae, Dinophyceae and Myxophyceae. Cultures were all grown at an illumination of 0.045 cals/cm^2/min at 18°C in the presence of excess nutrients and cropped during the "exponential" phase of growth. Full spectra of the sugars, amino acids and pigments present were determined. Although this is still only a very modest beginning, a few interesting facts have emerged, some of which are contrary to the classical idea of the composition of phytoplankton.

Carbohydrate was the principal "storage product" as opposed to fat, which was generally quite low in amount, especially in the diatoms. The exceptions were the two dinoflagellates studied which had a high fat content. The predominant sugar in all organisms was glucose, with lesser amounts of galactose and ribose always present. The amino-acid spectra of the proteins showed them to have quite a poor "protein quality" by mammalian criteria, with a predominance of the carboxylic amino-acids and of alanine and glycine. Of course, we have no knowledge yet as to whether these amino acids necessarily have a poor "protein quality" for the marine crustacea and other organisms that feed on the marine phytoplankton. One cannot help but be struck by the relatively similar composition of the "ash free" fraction of all these various classes of algae when they are grown with excess nutrients present.

The nature and composition of the cell walls of planktonic algae have had little direct study and much of our knowledge is derived from staining tests devised for terrestial organisms. There is no doubt that the Chlorophyta have a cellulose-like membrane, often quite strong, but it is far from certain that this membrane is necessarily a glucose polymer. Lewin (1958) found galactose and a uronic acid to be the main components of the cell wall of a Platymonas. This genus has a particularly tough membrane and rates a high crude fibre (Parsons et al, 1961). The dinoflagellates are also reported to be cellulose covered (we found a high crude fibre on Exuviella sp.) but I have seen no reference to the exact chemical identity of the envelope having been established by direct analysis. The position is even less clear with the diatoms. A large Coscinodiscus was found by us to have a high crude fibre content but Skeletonema costatum did not. Although Lewin (1955) reported a glucuronic acid polymer in the capsule of Navicula pelliculosa, this was only abundant under certain conditions and we have found only traces of hexuronic acids in the marine diatoms so far studied at Nanaimo. The surface sheath of the Cyanophyta seems to vary in nature from species to species, being described variously as "pectin" and "hemicellulose" and next to nothing is known of the nature of the cell walls of the flagellate Chrysophyceae and Xanthophyceae.

Finally, we should mention the possible food value of detritus, which is an important constituent of the ingested material of many benthic organisms and which can comprise over 80% of the particulate organic matter even in mid-ocean (McAllister et al, 1960; cf. also Allen, 1939; and Lisitzin, 1959). It is inconceivable that such material does not have some food significance to pelagic organisms and evidence to indicate this is implied by the work of Riley (1959b) and Marshall and Orr (1958a and 1958b). I have seen no reports of the detailed

analysis of detrital material or its structure and nature. The composition of the detritus at Ocean Station "P" was largely protein, with a little carbohydrate and less fat (McAllister *et al*, 1960). We have obtained a very similar analysis of detritus from the waters near the British Columbia coast during winter, when the amount of detrital matter was quite large and comparable in quantity to that found at Ocean Station "P" in summer. (It is interesting to note that, at the onset of the "spring bloom" of plants in March, the proteinaceous detritus at the coast largely disappears).

(b) Phytoplankton as food for zooplankton and fish

There is a serious shortage of any satisfactory knowledge of the nutritional requirements of the marine zooplankters or indeed their grazing habits and filtering rates. An excellent treatise on some aspects of these last two problems has been published by Cushing (1959), who enlarges on the "encounter" theory of grazing. This is not relevent to the immediate discussion except to stress the fact that realistic filtering rates and feeding habits must be known for a wide range of herbiverous zooplankton if we are to understand fully what I would term the phenomenon of "oceanic over grazing." It was noted by Beklemishev (1957) and others, and proved beyond reasonable doubt by McAllister *et al*, (1960) that in the *fertile northern* part of the Pacific Ocean, the plant standing crop is at a comparatively low level as a result of over grazing. However, at the coast, the standing crop of phytoplankton, in water of essentially the same fertility, can be at least fifty times as great as that in the open ocean and generally increases and decreases by "classical" cycles of blooming and grazing. The cause of this phenomenon, which may also be partly responsible for the "Island Mass Effect" (Doty and Oguri, 1956), is, in my opinion, one of the most important problems awaiting solution by zooplanktologists. It has an important bearing on the whole marine food cycle of this planet as the effect is found in many parts of the world. We are clearly dealing with the subtle interrelationships of zooplankton and phytoplankton. Their relative abundance at critical times of the year, itself a function of the depth of water, physiology of the animals, plant growth conditions (water stability nutrients and light) and the grazing behaviour of the zooplankters need to be much better known.

Turning now to the food value of phytoplankton for zooplankters, one can only make a few cautious generalizations, based largely on observations made with fresh water crustacea and the marine copepod *Calanus*.

The most obvious limiting factor is the size and shape of a phytoplankton cell in relation to the oesophagus of the animal feeding upon it. A cursory examination of a settled sample of plankton serves to illustrate the fact that many diatoms can be too large and unsuitably constructed for them to be utilized by what one would assume to be the prevalent zooplankton. In the autumn of 1960, a monomictic bloom of *Chaetoceros convolutus* persisted for many weeks in the Strait of Georgia, British Columbia, probably because there was nothing present in the water that would eat it. Indeed there was some evidence that the cells of this species could kill fish by sticking on to their gill tissues.

The young stages of *Calanus* find large *Coscinodiscus* cells and *Ditylum brightwellii* too big for ingestion, although the adult animal can probably manage most of the phytoplankton (Marshall and Orr, 1958a). There is certainly a lower limit of cell sizes in *Calanus* feed. Although the animal can utilize a *Chlamydomonas* sp. with cells 6-8 μ in diameter (Gauld, 1951), cells with a diameter smaller than 10 μ are filtered less readily than larger ones, and are used very inefficiently if less than 5 μ in size (Marshall and Orr, 1955b and 1958a). If the cells have a diameter of less than 2-3 μ (such as *Nannochloris*, bacteria and bacterial spores) they are not ingested at all. They may have potential food value if first eaten by phagotrophic organisms such as *Oxyrrhis* (Raymont and Gross, 1942; Fuller and Clarke, 1936; Marshall and Orr, 1955b). Small marine larvae probably use only those cells in the plankton which are smaller than 10 μ (Cole, 1952).

The enzyme systems of marine and fresh water phytoplankton feeders have been examined by a few workers. Lipase activity is present (Bond, 1934; Hasler, 1935) and, as might be supposed, proteinase activity is found to be considerable. I have seen no work designed to measure the suitability of various protein diets, although Fuller (1937) mentions that *Calanus fin-*

marchicus can make use of about half the nitrogen in Nitzschia closterium. Calanus was reported by Bond to have a proteinase activity at a pH as low as 3.5. This is quite contrary to the observations made by Hasler (1935) on the fresh water crustacea Daphnia magna and Daphnia pulex, which have trypsin-like enzymes. Hasler (1937) extended his work to a study of the dipeptidase, aminopolypeptidase and carboxypolypeptidase activities of Daphnia, Polyphemus, Diaptomus and a fresh water Calanus. It is not known to what degree his observations may apply to marine species.

There is general agreement that there are amylase enzymes present in the various animals studied but very little cellulase activity, (von Dehn, 1930; Bond, 1934; Hasler, 1935; Fish, 1955a; Huang and Giese, 1958). The absence of cellulase activity may also be inferred from the absence of attack on many plant cell membranes (ref. e.g. Gibor, 1956). Whole plant cells often pass through an animal gut unharmed, or if the content of a plant cell is digested it is only after having first passed out through pores in the cell wall. One cannot generalize, however, as Conover (1960) noted that Thalassiosira decipience passed unchanged through part of the gut of Acartia tonsa and then quite suddenly disintegrated. Calanus and other animals cannot digest alginic acids (Bond, 1934; Huang and Giese, 1958). However, vast more work is necessary before we can reach any satisfactory conclusions.

In particular we know next to nothing about the role played by intestinal micro-flora in the gut of planktonic crustacea (Huang and Giese, 1958).

There is probably a similarity between the diet of Calanus and many other members of the marine planktonic crustacea, with a good correlation between growth and egg laying and the overall abundance of phytoplankters (Marshall, 1924; Marshall et al, 1934; Digby, 1950; and Marshall and Orr, 1952). Studies using radioactive carbon by Marshall and Orr (1955a) and Lasker (1960) support the view that efficiency of phytoplankton utilization by crustacea is very high when the concentration of plant cells in the surrounding water is optimum. Skeletonema costatum is generally agreed to be an excellent diet.

All of the diatoms tested in feed trials by Marshall and Orr (1952 and 1955b) were found to be good food for Calanus finmarchicus although some were better than others. The two dinoflagellate species used were also satisfactory as was the coccolithophore Syrascosphaera carterae. On the other hand a marine Chlorella, the cryptomonad Hemiselmis rufescens and the Chrysophycean Dicrateria were very poor foods. Conover (1960) has recently added to our knowledge of the feeding of zooplankters using twelve species taken mostly from below 100 m. He characterized the animals as to whether or not they were herbivores or carnivores and tested the abilities of the herbivores to utilize species of diatoms in pure culture, most of which were readily digested. Bacteria were present so we do not know to what extent they provided critical growth factors. Corner (1961) measured the intake of carbohydrate, lipid and protein by Calanus helgolandicus from natural sea water. The organism ingested organic matter in preference to inorganic material in the same sample.

It is known that animals will show some discrimination when feeding on algal species with different nutritional values. There is even marginal evidence that a Calanus can be "conditioned" to favour one species more than another (Harvey, 1937).

Only by using bacteria-free cultures of both plant and animal can the true food value of a phytoplankter for a given zooplankter be correctly evaluated. There are regrettably few such studies. The classical work of this type is by Gibor (1956) who showed that there were very real differences in food value between various species of phytoplankton. Although a single species (Monochrysis lutheri) provided a balanced diet for Tigriopus (27 generations) it was generally necessary for several different species to be eaten together if the full growth and development of the animal was to be attained (Shiraishi and Provasoli, 1959a and 1959b). Provasoli et al, (1959) have given a useful list of algal diets for Artemia salina and Tigriopus japonicus, only a few of which were wholly satisfactory.

(c) Phytoplankters, as food for lamellibranchs

A certain amount of work has been done on the dietry requirements of lamellibranchs, mainly mussels, clams and oysters, because of their direct economic importance. These

organisms are among the few commercially important marine animals that utilize the marine phytoplankton algae directly and one of the most immediate practical applications of primary productivity research is in connection with the rearing and fattening of oysters and other shellfish.

Lamellibranchs, in particular oysters, seem capable of filtering out particles of 1-2 μ diameter or less by a mechanism still not very well understood (MacGinitie, 1945; Barker-Jorgensen, 1960). There is an optimum range of concentrations of food stuff in the water. At lesser concentrations the organism does too much work in feeding and at greater concentrations too much time and energy is spent in attempting to clean gills etc. (ref. e.g. Loosanoff, 1947; Pratt, 1955).

The nature and thickness of an algal cell membrane are again significant as both proteinases and cellulases are said to be in short supply in the lamellibranchs (Yonge, 1935; Coe, 1945 and 1948; Davis and Guillard, 1958). However, it is far from certain that the absence or shortage of cellulase activity is universal (Nelson, 1947; Morton, 1958) and cellulose can perhaps be used in another way. Nelson (1947) has suggested that cellulose particules act as a substrate for bacteria and these bacteria form the food for lamellibranchs ingesting the cellulose fragments. A plant cell can be digested, whatever its membrane, if it is small enough for phagocytic scavenging by blood cells in the lamellibranchs (ref. e.g. Yonge, 1935; and Coe, 1945). As with the crustacea, the shellfish seem to have a good supply of amylase and glycogenase enzymes (Coe, 1945).

Small diatoms may be digested by oysters but larger diatoms and the Chlorophyceae and Dinophyceae are expelled unchanged unless they are initially damaged (Bruce et al, 1940; Cerruti, 1941; Coe, 1945 and 1948). A long list of the ultra-plankters thought to have food value is given by Thorson (1946). Skeletonema again comes in for special mention. Davis and Guillard (1958) have made a much needed study of the dietary value of flagellates for oyster and clam larvae, using twelve species of algae from ten genera. Again differences in food value could be detected. Isochrysis galbana and Monochrysis lutheri were about equally beneficial for both larvae, but a Chlorococcum sp. was preferred by the clams. Somewhat better growth was experienced by both when a mixture of several algae were fed to them to give a "balanced" diet.

Certain lamellibranchs show a remarkable selectivity in their feeding. Nelson (1947) reports a case where a Chaetoceras was rejected by oysters feeding on skeletonema. The extraordinary degree of selectivity possible by oysters was demonstrated by Loosanoff (1949). Neither the size nor the shape of the food was a factor in this selection which was attributed to the presence of chemo-receptors on the labial palps.

It is possible that fresh plant food plays only a minor role in the nutrition of many lamellibranchs and other benthic filter feeders. Detritus, small protozoa and, most important, bacteria and molds undoubtedly constitute the main food supply of some animals. The apparent correlation between shellfish growth and the presence of a large standing crop of diatoms or dinoflagellates, both known to be useless as a direct food stuff, has long been puzzling. Inasmuch as the correlations reported in the literature are real the explanation presumably lies in the fact that large standing crops rapidly produce detritus and dissolved organic matter which is, in turn, used directly or as a substrate for bacterial growth (Nelson, 1947; Coe, 1948; Pratt, 1955; and Hanaoka, 1958).

(d) The nutritional significance of dissolved organic matter produced by algae

This brings me to the last and perhaps, in some sea areas, the chief significance of primary photosynthetic production, namely the role of algae in furnishing "dissolved" organic matter in the oceans.

The production of organic solutes by decomposing plankton needs little comment. This processes has never been studied in great detail, as has the formation of inorganic products, but we may infer that most of the soluble organic matter that is produced by dead cells is liberated rapidly, probably before they have time to sink much below the euphotic zone (von Brand et al, 1939; Spoehr and Milner, 1949; Skopintsev, 1949; Pratt, 1950; Golterman, 1960).

The results of the experiments by Krogh et al, (1930) gave rise to the belief that the amount of organic matter secreted by living algae was not very significant but more recent work is reversing this view. It is likely that many species in the phytoplankton, especially the small flagellates, produce large amounts of soluble carbohydrates, acids, peptides, etc. Perhaps more organic matter is produced whilst cells are alive than by their decay once dead (Aleyev, 1934; Kay, 1954; Bishop et al, 1954; Tolbert and Zill, 1956; Fogg and Wolfe, 1954; Lewin, 1956; Allen, 1956; Collier, 1958; Fogg and Boalch, 1958; Guillard and Wangersky, 1958; Wangersky, 1959; Wangersky and Guillard, 1960). The dissolved material thus produced has two functions, hormonal and nutritional.

Collier (1953) has described sea water in the following terms - "Neritic waters can be viewed much as the mammalian physiologist would view blood; as a transport system charged with living cells and agglomerates of proteinaceous and carbohydrate complexes, as well as dissolved gases. There is good reason for the marine biologist to approach from the point of view of blood chemistry."

By the direct production of water soluble growth factors (or their indirect production via the action of bacteria) plant cell secretions can influence the subsequent growth of other plant species with exacting nutritional requirements. Thus the observed succession of phytoplankton species in the sea is probably, in part, self-regulating. This subject has already been discussed fully by many workers. The hormonal and growth-factor significance of dissolved organic matter is equally important for the animal populations, however, and may be critical in deciding whether or not a given plant or detrital crop can be utilized to its fullest advantage.

The work of Collier and co-workers (1953 and 1956) has shown beyond reasonable doubt that the pumping rate and other physiological activities of lamellibranchs are influenced by the presence of dissolved organic material. The researches of Wilson have illustrated the differences which exist between various water masses in the development of eggs and larvae (ref. e.g. Wilson, 1951; Wilson and Armstrong, 1954). Although the Hardy "exclusion theory" may not be as significant in marine ecology as was once supposed, there is certainly evidence that plants secrete substances that repel or inhibit the feeding of planktonic crustacea (Lucas, 1936; Bainbridge, 1953; Ryther, 1954a) and influence the sinking rate of their eggs (Marshall and Orr, 1957).

Soluble organic matter may prove to be most important as a source of essential growth factors to supplement solid diets. Das (1960) has demonstrated how yeast extract and Vitamin B_{12} influences the early survival of fish larvae. Shiraishi and Provasoli (1959a and 1959b) showed by a most elegant series of experiments that growth factors (glutathione and vitamin mixtures) can supplement inadequate algal diets in the feeding of Tigriopus japonicus. The significance of this work cannot be over stressed as it seems to me most probable that certain monomictic blooms of phytoplankton may be useless as a source of food for zooplankters unless an adequate mixture of vitamin-like compounds is already present in the water. We have as yet no direct proof that this extreme state of affairs does occur in nature, but the possibility cannot be ignored.

The classical theory of Pütter (1909), that dissolved organic matter in sea water acts as a direct food stuff for animals, has been the subject of much controversy but seems to have been fairly convincingly disproven (ref. e.g. Krogh, 1931; Bond, 1933; Gellis and Clarke, 1935). However, it is far from certain that a measure of sustenance is not possible (Stephens and Schinske, 1961) especially from the larger colloidal particles (e.g. Gellis and Clarke, 1935; Fox, 1950; Morris, 1955) and the failure to recognize the importance of accessory growth factors may have invalidated some early conclusions. Recently Provasoli and Shiraishi (1959) have reported the rearing of Artemia salina entirely on soluble matter. They used a complex medium containing the essential additions of glutathione, thiamine and folic acid with particulate matter present to stimulate filtration. Conditions were of course, quite "unnatural" in that the concentration of organic matter was much greater than would generally be found in nature and the particulate matter (starch) may have adsorbed nutrients (Provasoli, personal communication) but the work illustrates the necessity of keeping an open mind on the question of direct absorption of organic substances.

Undoubtedly Pütter was correct in his appreciation of the food potential of dissolved or-

ganic material, even if the mechanism he suggested for its use may have been generally inapplicable. The amount of dissolved organic carbon in the sea may be as great as 20,000 mg/ m^3 at the surface although 2,000-3,000 mg C/m^3 is a more usual figure, with a rough oceanic average of around 1,000 mg C/m^3 (Fox et al, 1952; Kay, 1954; Plunkett and Rakestraw, 1955; Skopintsev, 1959; Duursma, 1960). The direct utilization of this carbon by micro-heterotrophs opens up a pathway for its re-entry into the food chain which, I believe, may prove to have considerable significance in the open ocean as well as in benthic areas.

Recent work by Jannasch and Jones (1959) has indicated that the number of bacterial cells in the sea is considerably higher than once supposed. From this and other work, together with reasonable assumptions as to the size and carbon content of marine micro-organisms, one can estimate that the mean standing crop of particulate carbon in the form of micro-heterotrophs is at least 0.1 mg/m^3 in the oceans of the world between 50°N and 50°S. Of course large variations occur, both horizontally and vertically, and in Arctic regions the amounts may be considerably less. Assuming a value of about 0.1 mg C/m^3 and a growth rate roughly comparable with that of phytoplankters, it can be reasoned that the heterotrophic production of organic carbon per cubic metre may be as much as 0.5-1% of the photosynthetic production in a moderate fertile ocean. When it is remembered that the depth of the total water column in the ocean may be fifty times that of the euphotic zone it will be seen that the heterotrophic production of carbon beneath unit area of ocean surface could be of the same order as the photosynthetic production.

The production of much of the organic particulate matter in the ocean can therefore result from heterotrophic processes, with the photosynthetic production in the upper layers acting as a replenishment mechanism for energy losses occurring in the various heterotrophic cycles. The net effect is greatly to increase the eventual utilization of photosynthetic primary production.

Work has been started at Nanaimo to attempt an evaluation of the importance of deep sea heterotrophic growth with a method using organic substrates labelled with radiocarbon (Parsons and Strickland, 1961).

Conclusions

There is little to be said by way of summary in a review such as this. I am sure that I have not done justice to a lot of good work that has gone into the study of steps in the marine food chain. Neththeless I am convinced that a more detailed and quantitative study of these steps, preferably under semi-laboratory conditions, should be the next phase of marine productivity research. Until it is undertaken, with something like the effort and support that we see given to descriptive and physical oceanography, a point will soon be reached beyond which no really satisfactory progress will be possible in solving the problems of fish growth in the sea.

The responsibility of those of us concerned with primary production is to see that we can describe the amount, nature, size and food potential of whatever plants are in the water and that we understand the growth kinetics of those plants as a function of light, temperature, salinity, and nutrition. Finally, it should not be forgotten that algae furnish the dissolved organic matter and much of the detritus in sea water. We must obtain a much better idea of the food potential of these important manifestations of organic production than we at present possess.

Research patterns in the field of primary productivity require a radical change if these objectives are to be realized and the work must be undertaken in close co-operation with those studying the herbivorous zooplankton.

A BIBLIOGRAPHY OF ARTICLES PERTINENT TO PRIMARY PRODUCTIVITY*

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Within the past ten years the number of notable articles on marine primary productivity has increased from less than a dozen per year to perhaps a hundred or more. This is an initial contribution toward a bibliography of this literature, i.e., a bibliography for the first dozen years of isotope use in primary marine productivity measurement.

In presenting this list of articles no attempt has been made to duplicate the lists of Klement & Wallen (1960) of 380 articles on the present and related fields. The papers by Strickland (1958b, 1960), Strickland & Parsons (1960) and Vinberg (1960) have further excellent bibliographies especially in respect to the more physical aspects of productivity. The articles have been selected for inclusion for various reasons, a major one being their being cited in the papers comprising the text of the accompanying volume. This does not pretend to be a complete or exhaustive bibliography, but it does have in it most of the papers of note published before 1960.

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