Organisms and the Composition of Sea Water

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Chemical Composition of Marine Organisms

Alterations of the concentration of the dissolved constituents of sea water are brought about by the development and subsequent death and disintegration of organisms. Virtually all of the substances extracted from the water are returned to solution by metabolic processes or by disintegration of the organisms, but the elements removed are returned to solution at some later time and often in some other part of the water column. Hence, the modifications may be in opposite directions at different times and localities. A small fraction of the organic remains accumulates on the sea bottom and is lost to the cycle.

Sea water probably contains in solution all of the chemical elements, although only some fifty have yet been detected. There is a large amount of data on the occurrence of various elements in marine plants and animals, but unfortunately the material is far from complete for any one biological group. Either a few elements only have been determined—such as iodine, for example, which has been thoroughly investigated—or only a portion of the organisms—for example, the skeletal structures—has been analyzed.

Vinogradov (1935, 1937) has compiled the chemical analyses of the lower plants and animals, both aquatic and terrestrial. He reports some sixty of the elements that have been found in one or more species. Webb and Fearon (1937) have tabulated thirty-nine elements that are commonly found and have divided these into two groups according to their apparent importance to living things: (1) eighteen invariable elements, and (2) twenty-one variable elements. These classes are further subdivided on the basis of the concentration in which the elements are present. Seven elements are listed as contaminants (table 46).

The primary invariable elements are the essential constituents of carbohydrates, lipides (fats), and proteins. Some of the invariable elements classed as secondary or as microconstituents are always present in the lipides and proteins. This list is for plants and animals in general and not for marine forms alone. Comparison of tables 46 and 36 shows that nine elements (starred) detected in organisms have not yet been

228

reported for sea water, and that seven (uranium, thorium, cerium, lanthanum, yttrium, scandium, and radium), known to occur in sea water, are not listed by Webb and Fearon.   Radium, at least, should be added to their list (p. 184).

TABLE 46
ELEMENTS CLASSIFIED ACCORDING TO THEIR DISTRIBUTION
AS PERCENTAGE BODY WEIGHT OF ORGANISMS
(Webb and Fearon, 1937)

Invariable (18)			Variable (21)		Contaminants
Primary 1–60%	Secondary 0.05–1%	Microconstituents <0.05%	Secondary	Microconstituents	
Hydrogen	Sodium	Boron	Titanium*	Lithium	Helium
Carbon	Magnesium	Fluorine	Vanadium	Beryllium*	Argon
Nitrogen	Sulphur	Silicon	Zinc	Aluminum	Selenium
Oxygen	Chlorine	Manganese	Bromine	Chromium*	Gold
Phosphorus	Potassium	Copper		Cobalt*	Mercury
	Calcium	Iodine		Nickel	Bismuth*
	Iron			Germanium*	Thallium*
				Arsenic	
				Rubidium	
				Strontium	
				Molybdenum	
				Silver	
				Cadmium*	
				Tin*	
				Cesium	
				Barium	
				Lead	

* Not yet reported for sea water.

The lack of comparable data for the different types of organisms makes it necessary to consider their composition under three headings— namely, organic material (largely carbohydrates, lipides, and proteins), inorganic skeletal structures, and inorganic solutes in the body fluids. Although the proportions of carbohydrates, lipides, and proteins may vary considerably, the composition of any one type is rather constant, so that the average values in table 47 can be used with some confidence. Furthermore, there are numerous determinations of lipides (ether extract) and protein (based on nitrogen determinations), and from these measurements and the loss on ignition the carbohydrate may be computed. Skeletal structures differ so much in composition and in their mass, compared to that of the organic material, that they must be considered separately.   Inorganic solutes in the body fluids are considered as a separate class, because they apparently do not differ very much in com-

position and concentration from the surrounding sea water; consequently, the presence of water in the original sample will give merely rather high values for the inorganic solutes. The great changes in relative composition are found in the organic material and skeletal structures, for which reason, if a mixed plankton sample containing sea water is analyzed, the results for the organic material and skeletal structures will not be materially affected if it is considered that all the sodium or chloride, as well as other elements in the proportions in which they occur in sea water, are in the body fluid or sea water.

TABLE 47

AVERAGE COMPOSITION OF ORGANIC MATERIALS

(In part from Rogers, 1938)

	Percentage composition			Relative proportions by weight, C = 100			
Element	Carbohy-drates	Lipides	Proteins	Element	Sea water	Lipides	Proteins
O........	49.38	17.90	22.4	C.......	100	100	100
C........	44.44	69.05	51.3	P.......	0.05	3.1	1.4
H........	6.18	10.00	6.9	N.......	0.5	0.88	34.7
P........		2.13	0.7	S.......	3150	0.45	1.6
N........		0.61	17.8	Fe......	0.07		0.2
S........		0.31	0.8				
Fe.......			0.1				

In table 47 are given the average compositions of the three great classes of organic material (Rogers, 1938) and the relative proportions in which their component elements occur in sea water. The oxygen and hydrogen are not considered, and the values are adjusted to C = 100. The values for C, S, and Fe are from table 36; those for N and P are the average winter values in the English Channel (pp. 252, 258). In the lipides, phosphorus is concentrated, and in the proteins the nitrogen and phosphorus show a great increase with respect to carbon. The fact that sulphur, which is one of the relatively abundant elements in sea water, is a minor constituent of the lipides and proteins in organic material indicates that carbon, here used as the reference element, is itself markedly concentrated. The values given in table 47 are general averages, and those for marine organisms may differ slightly. It should be noted that changes in the proportions of carbohydrates, lipides, and proteins will modify the ratios in which the above-mentioned elements will be removed from the water. Many of the other elements that are concentrated by organisms—for example, iodine, iron, and copper—probably form a part of the organic material or they occur in the skeletal structures, as it is difficult to see how the free ions could be retained in the body fluids

at such tremendously higher concentrations than those in the surrounding sea water.

In table 48 are given analyses of certain types of skeletal material. In each case there is some organic matter, which is highest in the lobster carapace, and even in the phosphatic brachiopod shell it forms a large fraction. Of course, there are wide ranges in the proportion of inorganic skeletal structures in the whole organism, and in some cases such struc-

TABLE 48

PERCENTAGE COMPOSITION OF SKELETAL MATERIAL

(Recalculated from Clarke and Wheeler, 1922)

Substance	Foraminifera (*Orbitolites marginatis*)	Coral (*Oculina diffusa*)	Calcareous alga (*Lithophyllum antillarum*)	Lobster (*Homarus* sp.)	Phosphatic brachiopod (*Discinisca lamellosa*)	Siliceous sponge (*Euplectella speciosa*)
Ca.............	34.90	38.50	31.00	16.80	26.18	0.16
Mg............	2.97	0.11	4.36	1.08	1.45	0.00
CO_3............	59.70	58.00	62.50	22.40	7.31	0.24
SO_4.............	....	....	0.68	0.52	4.43	0.00
PO_4.............	tr	tr	tr	5.45	34.55	0.00
SiO_2............	0.03	0.07	0.04	}0.30	0.64	88.56
$(Al,Fe)_2O_3$......	0.13	0.05	0.10		0.44	0.32
Organic matter, etc...........	2.27	3.27	1.32	53.45	25.00	10.72

tures may be entirely lacking. The first three examples are for calcareous types with $CaCO_3$ predominating, but in some groups $MgCO_3$ forms an important part of the shell. The lobster may be considered as representative of the arthropods in general, although the proportion of organic matter is probably even greater in the small forms. The amount of phosphate is notable in the lobster and even more so in the phosphatic brachiopod shell, which is predominantly calcium phosphate. The sponge spicules are virtually pure hydrated silica and may be taken as representative of the diatom and radiolarian skeletons. The silica, iron, and aluminum in the other analyses probably represent impurities introduced by the presence of clay and sand grains. These analyses cannot be regarded as complete, and further examination will undoubtedly reveal many other elements present in small amounts. It should be noted that chlorine and sodium, the two most abundant elements in sea water, are not shown in any of these analyses. These elements form soluble compounds and hence would not be suitable for skeletal structures. From table 48 it can be seen that the development or re-solution of skeletal structures of marine organisms may be expected to affect the concen-

trations of calcium, magnesium, carbon (as carbonate), sulphur, phosphorus, and silicon. Because of their relatively greater abundance in sea water, the distribution of magnesium and sulphur cannot be expected to show any appreciable effects of biological activity, but the distributions of the other elements mentioned do show certain features that can be attributed, in part at least, to the fact that they are important constituents of skeletal structures.

The relative concentrations of the elements that are abundant in the body fluids do not differ very much from those in sea water (table 49). Although little is known concerning the less abundant elements, it appears that the inorganic portion of the body fluids can be considered as slightly altered sea water. Therefore, this part of the organism cannot play any appreciable part in modifying the composition of the water. Although the composition and concentration of the inorganic solutes is of no particular importance in the present problem, these features have been studied intensively in problems of osmotic pressure relations (chapter VIII) and in connection with the mechanism of solute and water exchange between aquatic organisms and their environment. These fields have been reviewed by Rogers (1938).

TABLE 49

RELATIVE COMPOSITION OF BODY FLUIDS
(Adjusted to Na = 100. Data from Robertson, 1939)

Element	Sea water	*Echinus esculentus* (Sea urchin)	*Homarus vulgaris* (Lobster)	*Cancer pagurus* (Crab)
Cl..............	180	182	156	156
Na.............	100	100	100	100
Mg............	12.1	12.0	1.5	5.7
S in SO₄.......	8.4	8.5	2.2	6.7
Ca.............	3.8	3.9	5.0	4.8
K..............	3.6	3.7	4.7	4.0

Thus far only the various fractions of the organisms have been discussed, and it is of interest to consider the composition of the entire plant or animal. As the plants are the primary "consumers" of inorganic material, it would be desirable to know the composition of such important groups as the diatoms and peridinians, but no complete analyses of these forms have been made. What information we have will be discussed below. The data for animals is also far from complete, but in table 50 are given three examples. The relative compositions have been adjusted to Na = 100, and, for comparison, the constituents of sea water are given in the same way. The relatively high proportions of the elements abundant in sea water which occur in the copepod analysis

TABLE 50

RELATIVE COMPOSITION OF MARINE ANIMALS

(Adjusted to Na = 100)

Element	Calanus (Copepod) Vinogradov, 1938	Fish[a] (Average)	Archidoris britannica (Nudibranch) McCance & Masters, 1937–38	Sea water	Concentration factors		
					Copepod	Fish	Nudibranch
Cl	194	....	180	180	1.1	....	1.0
Na	100	100	100	100	1.0	1.0	1.0
Mg	5.6	36	156	12.1	0.46	3.0	12.9
S	25.9	259	7.1	8.4	3.1	31	0.85
Ca	7.4	52	262	3.8	1.9	13.7	69
K	53.7	383	20	3.6	15	109	5.5
Br	1.7	....	....	0.6	....	....	3
C	1113	ca. 4100	ca. 480	0.26	....	....	....
Sr	....	....	11	0.12	4,300	15,800	1,850
Si	1.3	....	....	0.001[b]	....	....	92
F	....	....	69	0.01	13,000	....	....
N	280	1276	107	0.001[b]	....	1,276,000	6,900
P	24.1	256	6	0.0001[b]	280,000	2,560,000	107,000
I	1.3	....	....	0.0005	241,000	....	60,000
Fe	0.04	1.3	0.23	0.0002[c]	80	6,000	....
Mn	1.3	0.0008	....	0.0001[c]	6,000	8	1,000
Cu	....	0.008	0.43	0.0001[c]	....	80	4,300

[a] From analyses of Jowett and Davies (1938), Clements and Hutchinson (1939).
[b] Winter values, English Channel.
[c] Higher values from table 36.

indicate the presence of considerable sea water in the original sample. As *Archidoris* possesses internal calcareous structures, the calcium content is high. Consequently the proportions of the elements constituting the organic material are rather low in these two cases. It is immediately obvious, however, that the essential constituents of the organic material, such as carbon, nitrogen, and phosphorus, are very high when compared to their relative concentrations in sea water.

If the relative amounts of the various elements in these animals are divided by their relative concentrations in sea water, a series of *concentration factors*, referred to sodium, are obtained. It will be seen that chlorine would give virtually identical results. The concentration factors range from about unity up to over two million for phosphorus in the fish, and in all three cases they are greatest for nitrogen and phosphorus. If it is assumed that the rates of diffusion of all substances and their rates of absorption by the organisms depend only upon the amounts of the ions in the water, then the concentration factors should be a measure of the time required to accumulate them. Those elements having the highest concentration factors would then be the ones that might limit the rate of growth. The data in table 50 indicate that nitrogen and phosphorus may very well be limiting elements in the sea, although it should be remembered that the examples are for animals that must obtain their supply of these elements either directly or indi-

TABLE 51

RELATIVE COMPOSITION OF PLANKTON ORGANISMS

Element	Sea water	Diatoms	Peridinians	Copepods	Concentration factors (referred to carbon)		
					Diatoms	Peridinians	Copepods
C.......	100	100	100	100	1	1	1
N.......	0.5[a]	18.2	13.8	25.0	36	28	50
P.......	0.05[a]	2.7	1.7	2.2	54	34	44
Fe......	0.07[b]	9.6	3.4	0.13	137	49	2
Ca......	1420	12.5	2.7	0.66	0.01	0.002	0.0005
Si......	0.4[a]	93.0	6.6	0.13	232	16	0.3

[a] Winter values, English Channel.
[b] Higher value, table 36.

rectly from the plants. If the total carbon in sea water had been used as the reference element, only nitrogen and phosphorus would have significantly larger factors. But it is obvious that carbon is itself concentrated more than one thousandfold with reference to the major elements in sea water. According to table 50 the relative concentration

in sea water of the following elements may be markedly affected by biological activity: carbon, silicon, fluorine, nitrogen, phosphorus, iron, and copper. Other elements might be included if the analyses were more complete or if other types of organisms were examined.

In table 51 are given the relative concentrations of certain elements in diatoms, peridinians, and copepods, adjusted to C = 100. The data for the photosynthetic forms are recomputed from Vinogradov (1935), and for copepods are the same as those given in table 50. The concentration factors for nitrogen and phosphorus are about the same in all three forms. In the diatoms, iron is higher, while silicon has the highest factor, which may indicate that these elements also limit the rate of growth. For the peridinians the factors for nitrogen, phosphorus, and iron are nearly the same.

Interrelations Between Elements Whose Distribution Is Affected by Biological Activity

Because the relative composition of organisms living in the sea differs from that of sea water, their growth will tend to modify the composition of the water. The ultimate regeneration of the inorganic substances by biological processes will return the elements to solution, but the net effects will usually be in opposite directions at different times and in different parts of the water column. Tables 50 and 51 show that certain elements present in the water in low concentrations, such as nitrogen, phosphorus, iron, and silicon, are those removed in the largest relative amounts. The distribution of these elements, known as the plant nutrients, is profoundly affected by biological activity, their concentrations are virtually independent of salinity, and they are commonly referred to as nonconservative, in contrast to those elements that bear a constant ratio to the total dissolved solids.

Plants are the most important "consumers" of the inorganic substances. Their activity is restricted to the upper layers of the sea (the euphotic zone), where there is adequate light for them to carry on photosynthesis. In nearshore areas the thickness of the euphotic layer may be only a few meters, and even in the open sea, where the transparency is great, the growth of plants is restricted to the upper few hundred meters (chapter XVI). Animals living below the euphotic layer may remove elements from solution which are necessary for the secretion of skeletal structures, but most of the materials must come directly or indirectly from plants that develop near the surface. The metabolic activities of the plants, animals, and bacteria return the elements to inorganic form. Part of the regeneration must occur in the euphotic layer, but there is a general downward movement of the particulate matter, either living or dead, and, consequently, a continuous transport of the elements away from the surface layer. As described thus far, it

would appear that there is a continuous drain upon the resources of the surface layers without any mechanism for renewing the store of essential elements in the euphotic zone. Precipitation and rivers contribute a certain amount of these elements, but this is negligible in comparison to the quantities that are brought up to the surface layers by processes of vertical diffusion, convection overturn, and upwelling. In regions where these processes are active, there is a plentiful supply of nutrients; consequently, such areas can support very large populations and are said to be very productive, in contrast to the open oceans, where there may be only a meager supply of nutrients.

Redfield (1934), following an earlier suggestion by Harvey, showed that regardless of the absolute concentrations a constant ratio exists between the nitrate-nitrogen and phosphate-phosphorus content of sea water, that these elements are apparently removed from the water by organisms in the same proportions in which they occur, and that on the death and decomposition of the organisms they are returned to solution simultaneously. Cooper (1938a) proposed a modified ratio, pointing out that the phosphorus data for sea water used by Redfield had not been corrected for salt error. Fleming (1940) obtained from examination of additional data a slightly different relationship for the N:P in plankton. All these figures are given in table 52, which also shows the relation of carbon to the other two elements in plankton.

TABLE 52

RATIOS OF C:N:P IN PLANKTON AND SEA WATER

Source	By weight			By atoms		
	C	N	P	C	N	P
Redfield (1934) Plankton............	53.2	8.2	1			
Redfield (1934) Seawater...........		9.0	1		20	1
Cooper (1938a) Seawater...........		6.8	1		15	1
Fleming (1940) Phytoplankton.......	42	7	1			
Fleming (1940) Zooplankton.........	40	7.4	1			
Fleming—Average: Plankton........	41	7.2	1	106	16	1

The ratios given above hold very well for the nitrate and phosphate in ocean waters (see fig. 51), but, since they represent the net effect of biological activity, marked deviations from the ratios may be found in individual types of organisms. However, they indicate the order of magnitude of the relationships in marine organisms.

In order to extend the usefulness of these relationships, it is worth while to add the oxygen. As an approximation, it may be assumed that two atoms of oxygen are required for the oxidation of each atom of

carbon, and that in photosynthesis the same amount is released for each atom of carbon converted to organic matter. Gilson (1937) has pointed out that the amount of oxygen should be increased about 25 per cent to allow for the oxidation and reduction of nitrogen, but we shall not introduce this factor. Therefore,

By atoms, $O:C:N:P = 212:106:16:1$

By weight, $O:C:N:P = 109:41:7.2:1$

In the euphotic layer, for each milligram of phosphorus utilized in photosynthesis, these ratios indicate that the plants will take up 7.2 mg of nitrogen (chiefly nitrate) and 76 ml of CO_2 and release the same volume of oxygen. At lower levels, where regeneration is taking place, the consumption of 76 ml of O_2 should set free the corresponding amounts of CO_2, N, and P. The oxygen saturation value for water of 5° temperature is of the order of 7.0 ml/L; hence it may be seen that, if all of the oxygen has been consumed in subsurface water of approximately this temperature, the NO_3-N and PO_4-P will be increased by about 50 μg-atoms/L (0.650 mg/L) and 3 μg-atoms/L (0.090 mg/L), respectively. These values are approximately the largest amounts ever encountered in the ocean. If all the waters leaving the surface were saturated with oxygen and completely depleted of nitrate and phosphate, it might be expected that there would be a close agreement in the deeper waters between these substances and the oxygen depletion (difference between the saturation value and the observed content). Such a general relationship exists in waters that have left the surface in lower latitudes, but in higher latitudes water sinking from the surface is saturated with oxygen and contains appreciable amounts of nutrients; hence the relationship between the oxygen depletion and the nutrient content must have the form

$$\text{Nutrient content} = V + \text{constant} \times O_2 \text{ depletion,}$$

where V is a variable amount in the water that sinks from the surface. In those regions in which there is a well-defined layer of minimum oxygen content at subsurface levels, layers of maximal nitrate and phosphate usually exist at or somewhat below the oxygen minimum.

The above comments do not necessarily apply to elements composing hard "inorganic" skeletal structures. Both calcium carbonate and silica are utilized by organisms in the euphotic layer and elsewhere, but the ratios of utilization of Ca, C as CO_3, and Si with reference to, say, phosphate-P, depend upon the character of the organisms. As pointed out elsewhere (p. 208), $CaCO_3$ is removed from the surface layers, and the same is true of the SiO_2. Although there is generally a depletion of Si in regions where the nitrate-N and phosphate-P are low, the processes of re-solution of calcareous and siliceous structures do not necessarily parallel decomposition and the regeneration of the elements found in
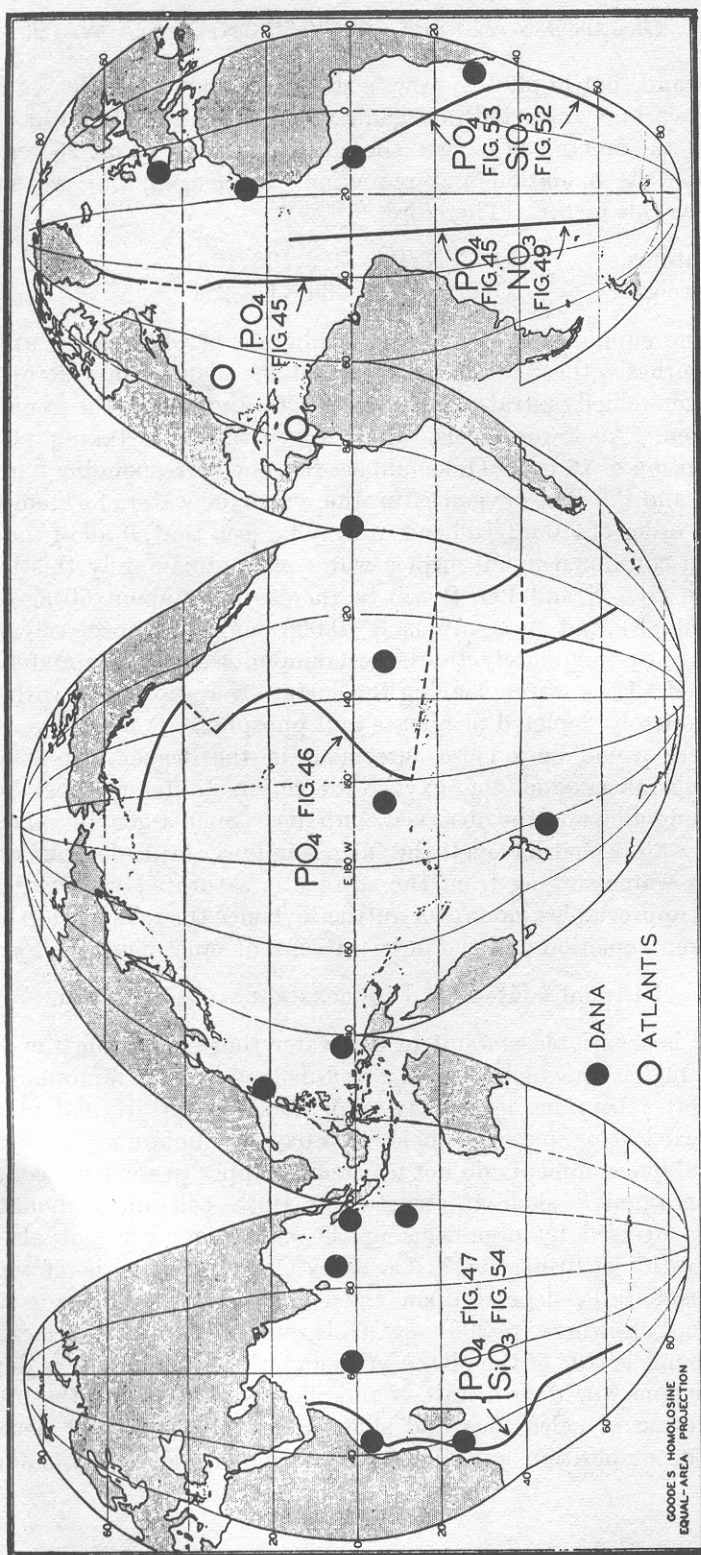
Fig. 44. Locations of vertical sections and stations used to illustrate the distribution of phosphate, nitrate, and silicate, in the oceans.

the soft parts of the organisms. Therefore, the general distribution of silicon in the sea differs somewhat from that of phosphate and nitrate, and the ratios between Si and N and Si and P are variable.

Distribution of Phosphate, Nitrogen Compounds, and Silicate in the Oceans

The distribution of phosphate in the three oceans may best be shown by means of longitudinal vertical sections whose locations are indicated
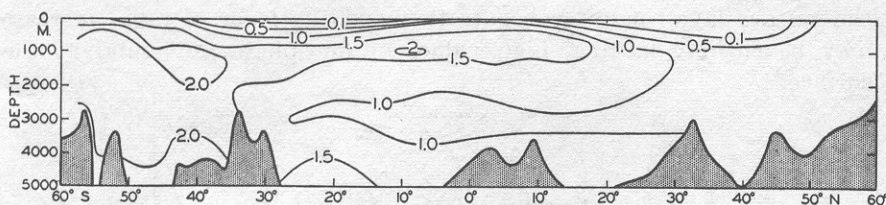
Fig. 45. Phosphate distribution in a longitudinal section in the central Atlantic Ocean. Units: μg-atoms of phosphorus per 20° liter.

in fig. 44. The representations are intended to bring out only the major features of the vertical distribution, and for this reason many of the minor irregularities have been omitted. The section in the Atlantic Ocean (fig. 45) is based on data obtained by the *Discovery* (Deacon, 1933) in the Southern Hemisphere, by the *Atlantis* (Seiwell, 1935) in the North Atlantic, and by the *Meteor* (Defant *et al*, 1936) in the area to the south of Greenland. The section in the Pacific Ocean (fig. 46)
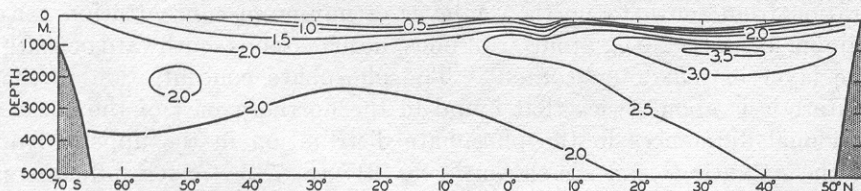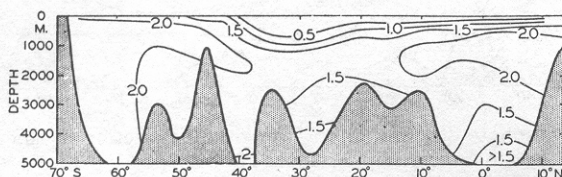

Fig. 46. Phosphate distribution in a longitudinal section in the Pacific Ocean. Units: μg-atoms of phosphorus per 20° liter.

has been constructed from *Discovery* observations in the Antarctic (Clowes, 1938) and from those of the *Carnegie* (in press). The section in the Indian Ocean (fig. 47) is based on *Discovery* observations (Clowes, 1938). Examination of these sections and the vertical distribution curves in figs. 48 and 50 shows that in general the distribution of phosphate and nitrate is characterized by four different layers: (1) a surface layer in which the concentration is low and relatively uniform with depth, (2) a layer in which the concentration increases rather rapidly with depth, (3) a layer of maximum concentration that is usually located somewhere between 500 and 1500 m, and (4) a thick bottom layer in which there is relatively little change with depth. Examination of figs. 45, 46, and 47 shows that the surface layer is thickest in mid-latitudes

in both hemispheres, that in these regions the layer of increasing concentration is clearly defined, and that the gradient is large. Associated with the divergences at and near the Equator, the surface layer is thin and the underlying gradient is very steep. This feature is brought out more clearly in fig. 198 (p. 710), which shows the vertical distribution of properties in the upper 300 m in a section across the equatorial currents in the Pacific Ocean. In high latitudes (above about 50°), where the surface layer of low concentration and the layer of rapid increase may be entirely lacking, high values of phosphate are found at the surface.

Fig. 47. Phosphate distribution in a longitudinal section in the western Indian Ocean. Units: μg-atoms of phosphorus per 20° liter.

In the Atlantic Ocean the highest phosphate content (about 2 μg-atoms/L) is found in an intermediate layer extending northward from the Antarctic and centered at depths of about 1000 m. At all depths of about 1000 m or more there is a gradual decrease in phosphate concentration from south to north. A layer of minimum concentration containing less than 1.0 μg-atoms/L of phosphorus extends southward beneath the layer of maximum content. The phosphate concentration in the Antarctic is about twice that found in the northern part of the ocean. Regional differences in the phosphate distribution in the upper 50 m of the Atlantic Ocean are shown in fig. 217 (p. 787). Such differences are of importance in the distribution of plankton. The variations in a transverse section across the South Atlantic are illustrated in fig. 218 (p. 788), which shows the variable thickness of the surface layer of low phosphate content.

The distribution of phosphate in the Pacific Ocean (fig. 46) has many features that differ from those in the Atlantic Ocean. As might be expected, the conditions in the Antarctic are rather similar. However, the maximum amounts in the Pacific are found not in the Southern Hemisphere, as in the Atlantic, but north of the Equator, where the amounts present are about twice those found in the Antarctic (3.5 μg-atoms/L and about 2.0 μg-atoms/L, respectively). Furthermore, there is no clearly defined layer of minimum phosphate content beneath the maximum. The deeper waters of the Pacific are in general higher in phosphate than those of the Atlantic Ocean. The difference in the character of the distribution in the two oceans is related to the nature

of the deep-water circulation (p. 754), which is also reflected in the lower dissolved oxygen content of the waters of the Pacific. The latter feature is particularly marked in the Northern Hemisphere.

The amounts of phosphate in the Indian Ocean (fig. 47) are greater than those in the Atlantic but somewhat less than those in the Pacific Ocean. The intermediate maximum in southern latitudes corresponds to that in the Atlantic, and the maximum in the equatorial region corresponds to that in the North Pacific, as it is related to the low oxygen content of the water. The minimum layer, at depths of about 3500 m, is clearly defined in all latitudes north of 40°S.

The differences between the phosphate concentrations in the three oceans are brought out in fig. 48, which is based on data collected by the *Dana* (Thomsen, 1931) on a voyage around the world and by the *Atlantis* in the western North Atlantic (Rakestraw and Smith, 1937). Observations from six stations (locations shown in fig. 44) in each ocean have been averaged and the values corrected for salt error (p. 182), so that they are somewhat higher than the values given in the sections. Too great emphasis should not be placed on the absolute values, as the purpose of the illustration is only to show

Fig. 48. Vertical distribution of phosphate in the Atlantic, Pacific, and Indian Oceans based on data from the stations shown in fig. 44.

the character of the vertical distribution in the three oceans, and to emphasize the higher phosphate content of the Pacific and the Indian Oceans in contrast to that of the Atlantic Ocean. Data from individual stations in moderate and low latitudes usually show a well-defined intermediate maximum.

The lack of nitrate observations from many parts of the sea makes it impossible to prepare sections comparable to those for phosphate. Considerable data have been collected by the *Dana* (Thomsen, 1931, 1937), the *Discovery* (Discovery Reports, 1932; Deacon, 1933), the
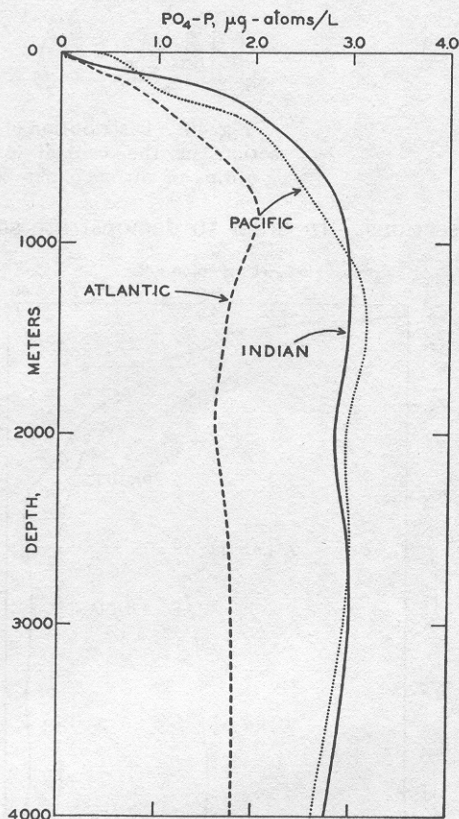
Meteor in the region to the south of Greenland (Defant *et al*, 1936) and by the *Atlantis*, but the information is insufficient to prepare longitudinal
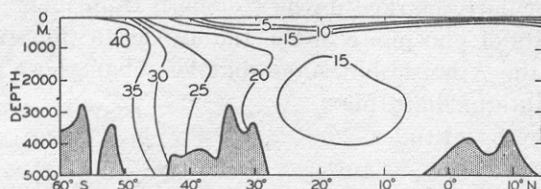

Fig. 49.   Distribution of nitrate in a longitudinal section in the central Atlantic Ocean. Units: μg-atoms of nitrogen per 20° liter.

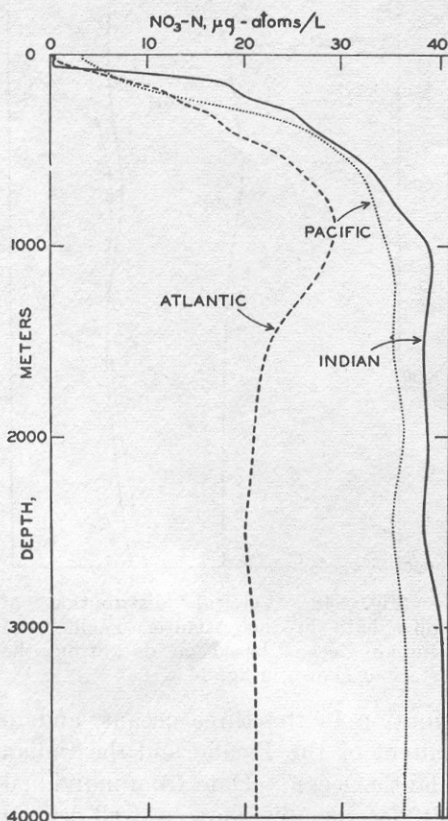sections.   In order to demonstrate some of the features of the nitrate

Fig. 50.   Vertical distribution of nitrate in the Atlantic, Pacific, and Indian Oceans based on data from the stations shown in fig. 44.

distribution, fig. 49 (from Deacon, 1933) has been prepared for the southern portion of the Atlantic Ocean. This corresponds in part to fig. 45 showing the phosphate distribution. As might be expected, there is considerable similarity between the patterns of phosphate and nitrate distribution, although the intermediate maximum is not clearly shown by the nitrate. The Antarctic is extremely high in nitrate. The data from the North Atlantic indicate that the character of the nitrate distribution is very similar to that of the phosphate—namely, that the concentrations are only about one half those present in comparable latitudes in the Southern Hemisphere.

Curves for the nitrate distribution in the three oceans based on observations of the *Dana* and *Atlantis* and comparable to those shown for phosphate are given in fig. 50. Too much emphasis should not be placed upon the absolute values, but the curves clearly demonstrate the characteristic features of the vertical distribution

and the high nitrate content of the Pacific and Indian Oceans in comparison with that in the Atlantic. Data from individual stations in moderate and low latitudes generally show an intermediate maximum somewhere between 500 and 1500 m.

It has repeatedly been emphasized that there is a close parallelism between the concentrations of nitrate and phosphate. This relationship has been demonstrated by plotting against each other in fig. 51 the average data for phosphate and nitrate presented in figs. 48 and 50. It is immediately seen that there is a good linear relationship between the two substances. The straight line represents the "normal" ratio of nitrogen to phosphorus of 15 : 1 atoms proposed by Cooper (1938a). Because of this relationship, it is possible to predict with a fair degree of accuracy the concentration of either nitrate or phosphate when either one is known, and, as pointed out previously (p. 237), a relationship exists between the concentrations of these elements and the oxygen depletion.
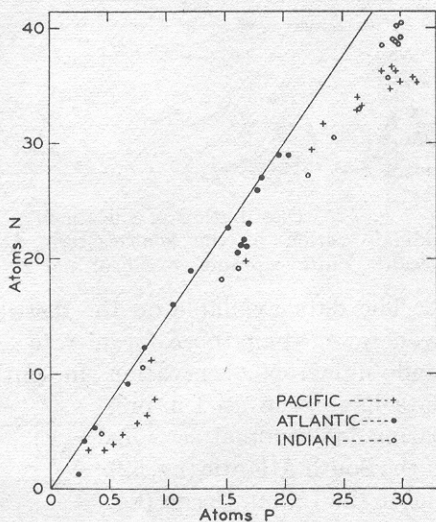

Fig. 51.   Relation between phosphate and nitrate in the three oceans. Points represent averages for individual depths used in constructing figs. 48 and 50. Straight line represents "normal" ratio proposed by Cooper.

The ranges in the various inorganic forms of nitrogen have been given (p. 181) as

$$NO_3\text{-}N = 0.1\text{--}43 \ \mu\text{g-atoms/L} = 1\text{--}600 \ \mu\text{g/L}$$
$$NO_2\text{-}N = 0.1\text{--}3.5 \qquad " \qquad = 0.1\text{--}50 \ "$$
$$NH_3\text{-}N = 0.35\text{--}3.5 \qquad " \qquad = 5\text{--}50 \qquad "$$

The nitrate is the most abundant form of inorganic nitrogen, and, as shown in fig. 50, the low values occur at and near the surface, the high values in deeper water.   The distribution of nitrite and ammonia, which are always in low concentrations, differs from that of nitrate in that the higher values occur in or above the thermocline.   Nitrite may also be found near the bottom in shallow water, but it is generally absent from most of the water column.   The ammonia content of the deeper waters is relatively uniform and low.   Data given by Rakestraw (1936) and by Redfield and Keys (1938) indicate that in deep water, away from shore, the amounts of these substances are small.   At one station, half way between Cape Cod and Bermuda, the nitrite was found only at about

75 m, and the ammonia varied irregularly from 0.3 to 0.6 µg-atoms/L between the surface and depths greater than 4000 m. Robinson and Wirth (193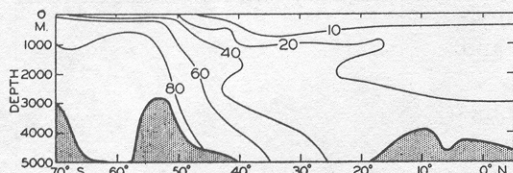4b) found that, off the West coast of Canada and Washington, ammonia was highest on the average near the surface (1.5 µg-atoms/L). Moberg and Fleming (1934) also found the ammonia to be rather irregular off southern California, but independent of depth and present in quantities of about 2.0 µg-atoms/L.

Fig. 52. Distribution of silicate in a longitudinal section in the southeastern Atlantic Ocean. Units: µg-atoms of silicon per 20° liter.

The data available on the distribution of silicate in the oceans are even fewer than those for nitrate. The *Discovery* (Clowes, 1938) has made numerous observations in southern latitudes, and certain of these data have been used in preparing longitudinal sections in the South Atlantic (fig. 52) and in the Indian Ocean (fig. 54). The locations of these sections are shown in fig. 44. The *Carnegie* obtained numerous observations in the northeastern and central Pacific and there are

Fig. 53. Distribution of phosphate in a longitudinal section in the southeastern Atlantic Ocean. Units: µg-atoms per 20° liter.

scattered observations from other regions, but they are inadequate for the preparation of longitudinal sections. In order to bring out similarities and differences in distribution, the silicate sections should be compared with the corresponding phosphate sections (figs. 47 and 53). It is
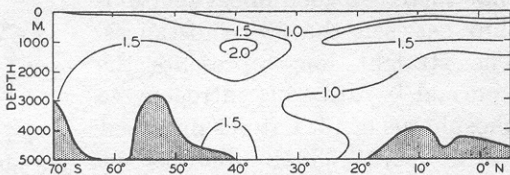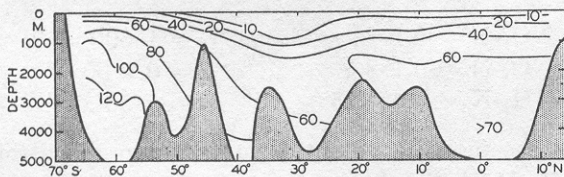

Fig. 54. Distribution of silicate in a longitudinal section in the western Indian Ocean. Units: µg-atoms of silicon per 20° liter.

readily seen that the vertical distribution of silicate differs from that of phosphate and nitrate, as there is no marked intermediate maximum and the concentration increases all the way down to the bottom. The reasons for this difference in the pattern of distribution have already been set forth (p. 237). In the Atlantic Ocean (fig. 52) the silicate content of the deeper water is much less in low latitudes than it is in the

far south, but in the Indian Ocean (fig. 54) the contrast is not so great. Data in fig. 55 indicate that the waters of the North Pacific are extremely rich in silicate and contain amounts comparable to those in the Antarctic. The Antarctic region is high in silicate, and also in phosphate and nitrate. Details of the distribution of silicate in the upper layers in the equatorial part of the Pacific Ocean are shown in fig. 198 (p. 710). The *Dana* made no silicate determinations, and it is therefore impossible to present vertical distribution curves for the three oceans comparable to those for phosphate and nitrate. The high content of silicate in the North Pacific is shown by two curves (Thomp-

son, Thomas, and Barnes, 1934, Barnes and Thompson, 1938) in fig. 55. The amount present below 1000 m (about 170 μg-atoms/L) is somewhat greater than that found in the Antarctic (Clowes, 1938). In order to demonstrate the lower quantities present in the Atlantic and Indian Oceans, curves were constructed from data in fig. 52 at 36°S and in fig. 54 at 2.5°N.

In basins, the distributions of the elements discussed above may be quite different from those characteristic of the open sea. As shown in chapter IV, the conditions in basins depend upon the topography, the character of the renewal processes below sill depth, and the dissolved oxygen content (aeration) of the water. In well-aerated

Fig. 55.   Vertical distribution of silicate at individual localities in the North Pacific, South Atlantic, and Indian Oceans.

basins, where there is inflow at the surface, the nutrient content is usually low. For example, in the Mediterranean Sea the phosphate and nitrate below sill depth are small when compared with the concentrations in the waters of the Atlantic Ocean (Thomsen, 1931). In the western Mediterranean below about 1000 m the contents of phosphate and nitrate are constant in amounts of 0.6 μg-atoms/L and 11 μg-atoms/L, respectively, which are about one half or less of the amounts in the open Atlantic. The dense water that flows out of the Mediterranean over the sill and mixes with the intermediate waters of the North Atlantic is therefore relatively low in nutrient elements and tends to reduce the phosphate and nitrate contents of the waters at intermediate levels in the eastern North Atlantic.
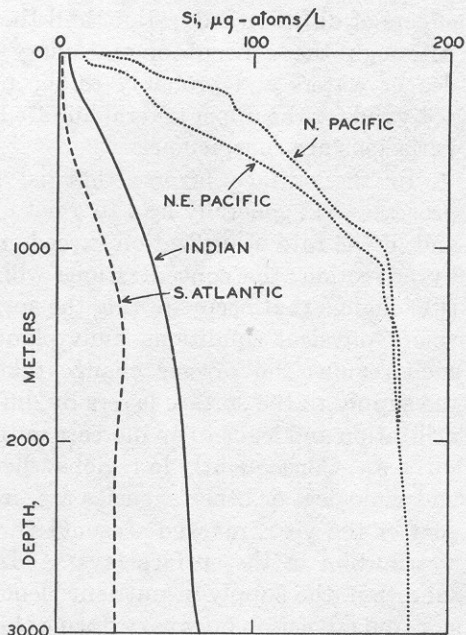
In basins of low oxygen content, such as the Red Sea, the nitrate and phosphate are relatively high for reasons already stated (p. 237). In stagnant Norwegian fjords, where hydrogen sulphide is present in the water, Ström (1936) found the phosphate to be as high as 10 μg-atoms/L.

Factors Influencing the Distribution of Nutrient Elements

The concept of dynamic equilibrium (p. 160) can be applied to the large-scale distributions of phosphate, nitrate, and silicate discussed above. On this assumption the distribution is stationary, the local change is zero, $(\partial s/\partial t = 0)$, and there must be a balance between the effects of diffusion, advection, and the net effects of biological processes. Although the concept of stationary distribution is applicable to the deeper waters and probably to the upper layers in low latitudes, it is not valid for the upper several hundred meters in localities where seasonal variations are conspicuous.

In the surface layers—that is, in the euphotic zone—biological processes will generally lead to a net utilization of the nutrient elements, and, if the rate of utilization exceeds the rate of supply by diffusion and by advection, the concentrations will decrease. This is the character-istic change that occurs during the spring and summer months in regions where physical conditions limit plant activity during the winter. In such regions the reverse change takes place during the winter, when the supply to the surface layers by diffusion and advection outweighs the utilization and leads to an increase in the nutrient content at and near the surface. Consequently in regions where the temperature, light intensity, and biological or other agencies are unfavorable for plant growth during part of the year, marked seasonal variations may occur in the nutrient distribution in the surface layers. In addition to fluctuations in con-sumption, the supply of nutrient elements to the surface layers by diffu-sion and advection may vary during the course of the year. For example, the magnitude of the vertical coefficient of eddy diffusivity, A_z, is inde-pendent of the gradient in the nutrient concentrations but will be affected by the temperature distribution and the wind conditions. Furthermore, changes due to shifts in currents will affect the distributions, although undoubtedly the most conspicuous effects are those related to vertical advection. In regions of surface convergence, waters low in nutrients may extend for a considerable distance below the euphotic layer. On the other hand, where there is divergence—that is, upwelling—nutrient-rich waters are carried upward toward the surface. Divergence may occur in the open ocean, as on the Equator and at the northern boundary of the Equatorial Countercurrent (p. 635), or along continental coasts where the prevailing winds are such that upwelling is induced (p. 501). In coastal areas where upwelling is seasonal or intermittent, the nutrient

content of the surface waters may show marked fluctuations and may actually increase during the season of maximum plant activity. In the discussion of the annual cycle of temperature in the upper layers, data were presented for Monterey Bay, California, where temperature changes due to the effects of heat conduction by eddy processes, upwelling, and current shifts could be traced (fig. 32 and p. 131). Corresponding data (Phelps, 1937) for the silicate distribution in Monterey Bay are given in fig. 56. In order to demonstrate the similarity to the temperature changes, the silicate scale in the diagram increases downward. During the spring and summer months, upwelling maintains a virtually constant amount of silicate in the surface layers despite the utilization that must take place, and at a depth of 20 m the silicate actually increases during this period. This seasonal variation is very different from the changes found in the English Channel (see fig. 66) and at Friday Harbor, Washington (see fig. 65), where there are much smaller concentrations of silicate during the summer than during the winter. The shift of the currents at Monterey Bay in September, which brings offshore water toward the coast, is reflected in a sharp drop in the silicate content and a corresponding rise in the temperature of the upper layers. A

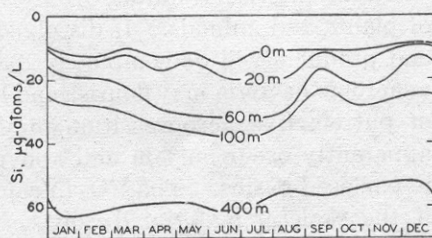Fig. 56. Seasonal variations in the silicate content at various depths in Monterey Bay, California. Silicate scale increases downwards.

similar effect is shown in December, when the northward-flowing coastal current is established.

From the foregoing comments, it is obvious that seasonal variations in the distribution of the biologically affected elements must be interpreted with great care. Fluctuations in concentration cannot be ascribed to biological processes alone unless it can be established on the basis of other data, such as temperature and salinity observations, that the effects of advection and diffusion can be neglected. In certain regions where there are marked differences between the summer and winter concentrations, estimates of organic production have been made from the depletion of nutrients occurring in the upper layers. Such estimates are minimal unless the effects of regeneration and diffusion are taken into account, and will be invalid if advection is an important factor, as in Monterey Bay. No systematic study of the seasonal variations in the distribution of the nutrients in the open ocean has yet been made, but in certain coastal areas a considerable amount of data has been accumulated that will be taken up under the discussion of the individual elements in the following pages.

Compounds of Carbon, Nitrogen, Phosphorus, and Silicon in the Sea

ORGANIC CARBON. The carbon present as carbon dioxide and the salts of carbonic acid, as well as many of the effects of biological activity on the distribution of CO_2, have been discussed in chapter VI. Seasonal changes in the CO_2 content of the waters of the English Channel have been described by Cooper (1933). The carbon present in sea water in organic combination will now be considered.

The CO_2 that is removed from the water by organisms is utilized partly for the secretion of calcareous structures but chiefly for building up organic compounds. Metabolic activity returns most of the organic carbon to solution as CO_2, and bacteria and other microorganisms play an important part in the break-down of excretory products and the detrital material resulting from the death and partial disintegration of plants and animals. If dissolved oxygen is present in the water, the end products will be completely oxidized, but in the absence of oxygen anaerobic bacteria may flourish and hydrogen sulphide and other products of putrefactive decomposition may be formed. The latter conditions apparently occur only in and above the sediments in certain areas and in enclosed basins. The CO_2 in calcareous structures returns to solution if the skeletal material dissolves. It should be remembered that, as with other elements, the cycle of carbon in the sea is not completely closed, since there is some loss to the sediments in both calcareous material and in resistant organic matter.

Before proceeding to a discussion of the amounts of carbon occurring in organic combination, either in living organisms or in particulate or dissolved compounds of organic origin, it should be pointed out that the division of the organic matter into various fractions is an empirical one. It has been customary to speak of "net plankton"—usually that which can be removed from the water by filtration through a fine net; "nanno-plankton"—that which will pass through the ordinary net but which can be removed by centrifuging or passage through filter paper; and "dissolved organic matter"—that which will pass through the filter. Examination of the literature reveals that a variety of methods have been used to separate those fractions, and consequently the results for different fractions are not always comparable. In the following discussion the term "particulate material" will be used to designate all the material, either living or dead, which is caught by a fine filter that will retain particles of about the size of the larger bacteria. It should be kept in mind that the organisms in sea water, the number of bacteria, and even the inorganic constituents involved in bacterial development undergo rather rapid changes after the collection of samples. Therefore, unless the separation into the required fractions is made immediately, or unless suitable preservatives are added, the results obtained for the

different fractions may be in error. Such errors may account for the relatively low amounts of particulate organic matter sometimes reported.

Pütter (p. 912) maintained that marine invertebrates obtained nourishment from the dissolved organic matter in the water. This hypothesis was based on observations which indicated that the amount of organic matter in solution was many hundred times greater than that present as plankton and particulate detritus. Further investigation has tended to reduce the difference between the two fractions of organic matter, because the earlier determinations of dissolved organic material were obtained by inaccurate methods. Additional studies summarized by Krogh (1931) and Bond (1933) also indicate that dissolved organic matter cannot be utilized by animals. Although Pütter's hypothesis has lost its original significance, it has stimulated a great deal of interest in the problem of the dissolved organic material and its utilization, and investigations have shown that dissolved organic material, although unused by animals, can be utilized by bacteria (p. 912).

Although the problem has attracted much discussion and speculation, there are very few trustworthy data concerning the amounts of carbon present in particulate or dissolved material in the sea. It is extremely difficult to determine accurately the carbon in small amounts of organic matter, especially in the presence of large quantities of salts. Methods have been proposed for concentrating the particulate material by filtration or precipitation (von Brand, 1935) and for determining the carbon by a microcombustion method. No method is as yet available for concentrating the dissolved organic material and freeing it from the salt; consequently the existing methods are based on wet combustions with strong oxidizing agents such as permanganate or chromate. (Bond, 1933; Krogh and Keys, 1934.) Two difficulties are inherent in the latter type of determination: (1) many of the inorganic salts present in sea water interfere with the oxidation and usually tend to give high values, (2) there is uncertainty as to the completeness of the destruction of the organic compounds. Some organic materials may be completely converted into carbon dioxide, water, and so on, by such a procedure; other compounds are only partially decomposed, and still others are not attacked at all. As the chemical constitution of the dissolved material is not known, it is difficult to evaluate the accuracy of determinations made by such methods. Determinations made by wet combustion give the "oxygen consumed," and a further uncertainty arises when it is necessary to convert these values into the amounts of organic carbon present in the samples.

The development of marine bacteriology has offered a new approach to the problem of the amount of organic material (both particulate and dissolved) in sea water. If sea water is placed in clean, stoppered bottles and kept in the dark, bacteria will develop in great numbers

and the dissolved oxygen will be consumed in metabolic processes. The amount of oxygen consumed, if it is not completely exhausted, is a measure of the amount of organic matter attacked by the bacteria. Even if the water is passed through an ultrafilter to remove particles of colloidal dimensions, and is inoculated with unfiltered sea water, it is found that enough organic matter is still present to permit the development of a large bacterial population. This problem has been discussed by Keys, Christensen, and Krogh (1935) and in a number of publications by Waksman and by ZoBell (for example, Waksman and Renn, 1936; ZoBell, 1940). Although a line of investigation of great promise, studies of bacterial oxygen consumption are beset with many difficulties and the results thus far available are not conclusive. It has been shown that the amount of oxygen consumed is a function of temperature, time, the source of water, and the solid surface-volume ratio (ZoBell and Anderson, 1936). Until standardized methods are established and extensive studies made of the regional, depth, and time variations of this property, only some general quantitative results given below can be considered.

The amount of carbon present in oceanic sea water in inorganic compounds is between 2.1 and 2.5 mg-atoms per liter (25 to 30 mg/L), depending upon the salinity, temperature, and effects of biological activity. Krogh (1931, 1934a,b) has summarized the available data on the amount of organic carbon in sea water. In his later work he reports total organic carbon analyses on six water samples from the Atlantic Ocean. Virtually no variation with depth was found, and Krogh considers the average value applicable to all depths and oceans. The average was 0.2 mg-atoms (2.05 mg) of carbon per liter, which is approximately one tenth of the amount present in inorganic form. From estimates of the amount of plankton, Krogh found the dissolved material to be about three hundred times more abundant than the particulate organic matter. These figures apply to the deeper water of the open ocean. Bond (1933) examined the surface layers in nearshore areas of higher production and found rather different values. His original data, obtained by wet combustion, are expressed in terms of oxygen consumed. In order to make them comparable to those of Krogh, it has been assumed that two atoms of oxygen were required to oxidize one atom of carbon. The recomputed minimum, maximum, and average values are given in table 53. Although Bond's values for the dissolved fraction are approximately the same as those of Krogh for the total carbon, they show a considerable range. Furthermore, it will be noted that the particulate material is relatively more abundant and forms between one tenth and one third of the total.

The results of bacterial oxygen-consumption studies are difficult to evaluate because of the variety of techniques that have been used.

Sometimes the water has been filtered and at other times it has not, and in relatively few cases have the cultures been kept for a sufficiently long time. The *maximum* values of oxygen consumption for unfiltered sea water range between 0.13 and 0.18 mg-atoms of oxygen per liter (1.5 and 2.0 ml/L). Using a 2:1 ratio by atoms, these are equivalent to 0.07 to 0.09 mg-atoms of carbon. These values are of the order of one fifth to one half of the total organic carbon values given above. Waksman and Renn (1936) have found that in the laboratory about 50 per

TABLE 53

ORGANIC CARBON CONTENT OF WATER NEAR FRIDAY HARBOR

Substance	mg-atoms/L of carbon		
	Minimum	Maximum	Average
Net plankton	0.008	0.06	0.03
Nannoplankton	0.005	0.11	0.03
Dissolved	0.13	0.25	0.20
Total organic	0.143	0.42	0.26

cent of the organic matter is readily attacked by bacteria, of which about 60 per cent is oxidized and 40 per cent is converted into bacterial cell substance. Estimates of organic carbon in sea water obtained in this way therefore give values of the same magnitude as those obtained by chemical methods.

The oxygen consumptions given above were for water from near the surface in areas relatively rich in plankton. Samples from deeper levels consume about one half as much oxygen. As shown previously (p. 236), there are relatively constant ratios between carbon, nitrogen, and phosphorus in the organic material. This fact has been used in certain studies in which the organic nitrogen (determined by the Kjeldahl method) is used as a measure of the amount of organic matter. The

Fig. 57. Annual cycle in the nitrate and nitrite content of the surface waters at Friday Harbor, Washington.

relative amounts of organic nitrogen and phosphorus in sea water are in fair agreement with the amounts of carbon given above. The organic nitrogen content of bottom samples (p. 1010) has been widely used as a measure of their content of organic matter. In sediments the ratio of
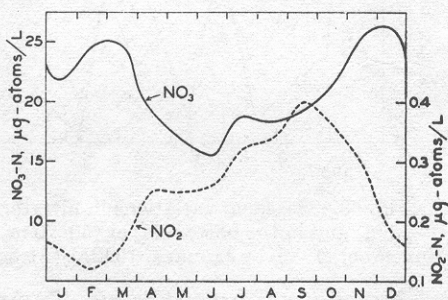
carbon to nitrogen has been found to be larger than in the organisms. This change in the ratio indicates that a relatively large proportion of the nitrogen has been lost by the refractory detrital matter that accumulates on the sea bottom.
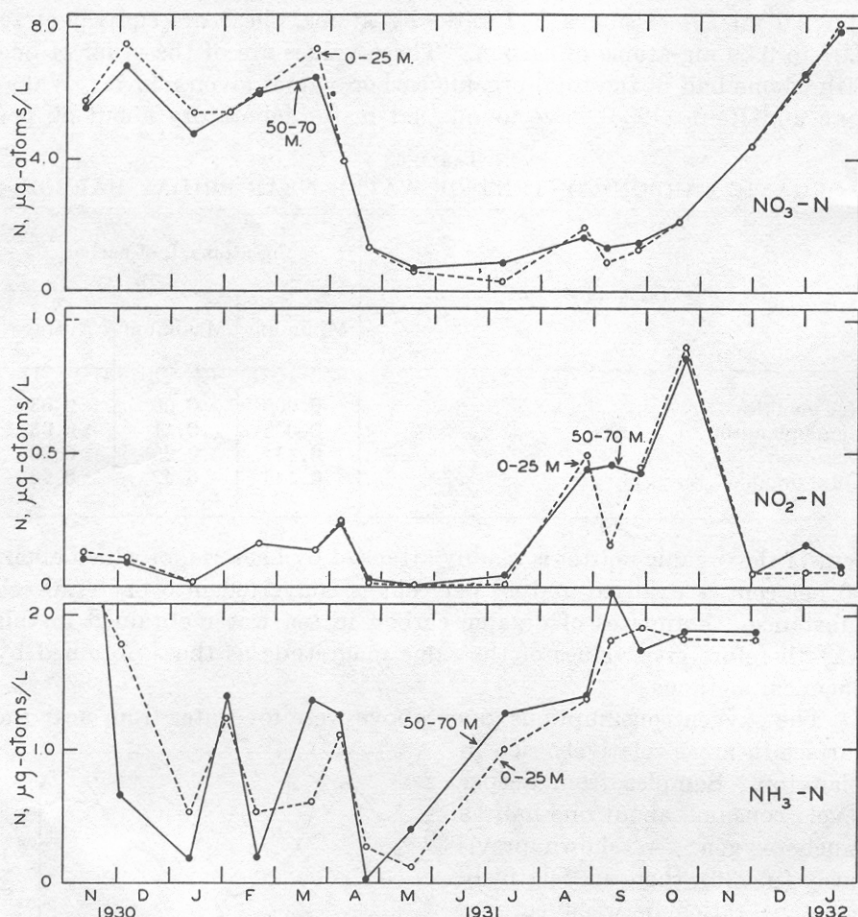

Fig. 58.   Seasonal variations in nitrate, nitrite, and ammonia in the surface layer (0–25 m) and in the bottom layer (50–70 m) in the English Channel during the period November, 1930, to January, 1932.   (After Cooper, 1937b.)

NITROGEN COMPOUNDS AND THEIR SEASONAL VARIATION.   In certain coastal areas, sufficient data are available to examine the seasonal changes in the distribution of nitrate, nitrite, and ammonia.   Only selected cases of seasonal variations will be given, but additional references may be found in the works cited.   Phifer and Thompson (1937) give the results of nearly five years' studies of the surface conditions at Friday Harbor, on the San Juan Channel.   The averages of the monthly means for NO_3 and NO_2 for the period 1931 to 1935 are shown in fig. 57.   It should be noted

that the NO_2 scale is one fiftieth that for the NO_3.   The nitrite appears in greatest abundance after the period of most rapid utilization of nitrate by plants in the spring and summer, and then decreases and is minimal at approximately the period of maximum nitrate.   Cooper (1937b) has shown the seasonal changes in NO_3, NO_2, and NH_3 in the surface (0 to 25m) and bottom (50 to 70m) layers in the English Channel during the interval November, 1930, to January, 1932 (fig. 58).   The three components are on different scales—namely, NO_3-N : NH_3-N : NO_2-N = 8 : 2 : 1.   In general, these data show cycles similar to those in fig. 57. During and after the period of greatest plankton development, there is a
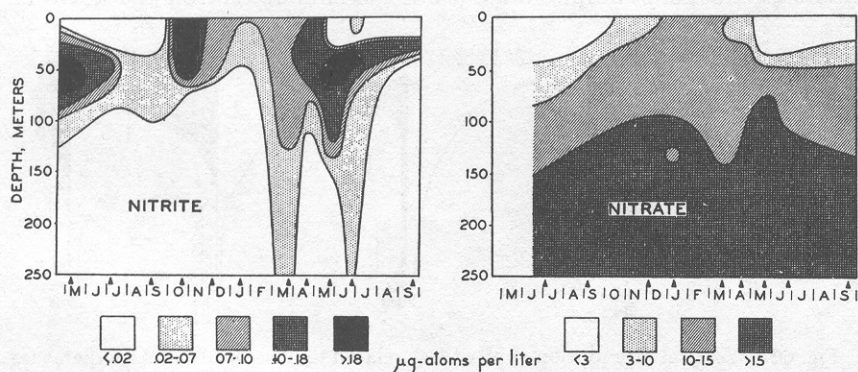

Fig. 59.   Seasonal variations in the vertical distribution of nitrite and nitrate in the Gulf of Maine during the period May, 1933, to September, 1934.   (After Rakestraw, 1936b.)

rise in ammonia, followed by one in nitrite and then one in nitrate. This indicates that, in the regeneration of nitrate from organic matter, the nitrogen passes through these stages.   It should be noted, however, that the ammonia and nitrite never reach concentrations as great as the nitrate.   In the English Channel the total inorganic nitrogen compounds are always much lower than at Friday Harbor.   Rakestraw (1936) has presented detailed observations of the variations in nitrite and nitrate during a year in the Gulf of Maine, from which fig. 59 is taken.   These data show the nitrite to be most abundant near the surface during the summer and autumn, when the nitrate is lowest.   That the higher quantities of nitrite are definitely associated with the distribution of density, and hence of temperature, is shown in fig. 60 (Rakestraw, 1936).   When there is a marked thermocline, the nitrite is either in or above it.   Similar data are not available for ammonia in the Gulf of Maine, but Redfield and Keys (1938) report that it is closely related to the amount of nitrite and also to the amount of plankton in the water.

The nitrogen in particulate organic material may be determined on the separated material which has been concentrated by filtration or

carried down with a flocculent precipitate (von Brand, 1935). Von Brand (1938) has determined the particulate organic nitrogen for five oceanic stations in the northwest Atlantic. The greatest variability was found in the upper 400 m, with values ranging between about 0.07 and 1.3 μg-atoms/L. The high values usually occurred at or near the surface. Near Iceland, values as high as 5.2 μg-atoms/L of nitrogen have been found, and in the Gulf of Maine surface values of 2.4 μg-atoms/L were obtained (von Brand, 1937). Below 400 m the amounts varied rather irregularly between 0.07 and 0.21 μg-atoms/L. Cooper (1934) found between 0.3 and 0.7 μg-atoms N/L as net plankton in the English Channel. Cooper's samples did not include nannoplankton and detritus.
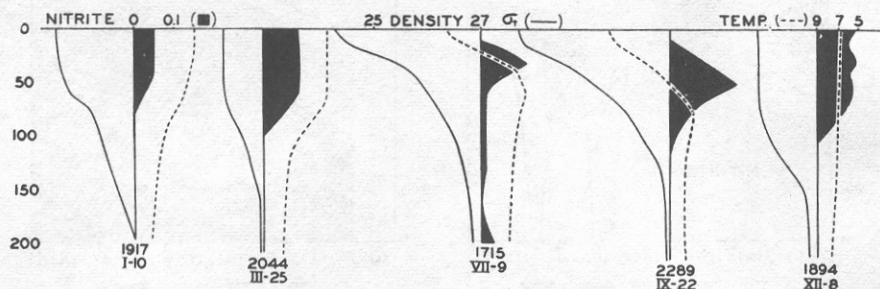

Fig. 60. Vertical distribution of nitrite, as related to density (σ_t) and temperature. (After Rakestraw, 1936.)

The total organic nitrogen, including both particulate and dissolved material, has been investigated by Robinson and Wirth (1934a,b). Kjeldahl analyses on unfiltered oceanic sea water showed about 7.2 μg-atoms/L of organic nitrogen near the surface, about half this amount at intermediate depths, and a slight increase again toward the bottom. In nearshore water the values near the surface were about twice as high as those in the oceanic samples. Moberg and Fleming (1934), using a similar method, found about 10 μg-atoms/L, on an average, of organic nitrogen in the surface layers off southern California and somewhat higher values at greater depths.

Figures 57 and 58 show that at Friday Harbor about 10 μg-atoms/L of NO_3-N disappear during the summer, and that the change in the English Channel is approximately the same. As NH_3 and NO_2 are rarely present in comparable amounts, we must conclude that the nitrogen is in organisms, organic debris, dissolved organic compounds, or in some unrecognized inorganic form.

Interesting experiments by von Brand, Rakestraw, and Renn (1937, 1939) on the regeneration of nitrate from marine plankton *in vitro* indicate that the formation of ammonia from organic matter probably takes place without the formation of intermediate compounds. The results

of one of their experiments are shown in fig. 61. In this experiment, sea water, with added diatom material, was placed in the dark. After about four months, much of the particulate-N had been converted to NO_3 through the intermediate stages of NH_3 and NO_2. The jars were then placed in the light and inoculated with diatoms. Almost complete utilization of the NO_3 followed. The jars were again placed in the dark and the cycle was repeated.

These experiments are extremely interesting, although regenerative processes *in vitro* apparently differ considerably from those in the sea. This result might well be expected from the peculiar laboratory conditions
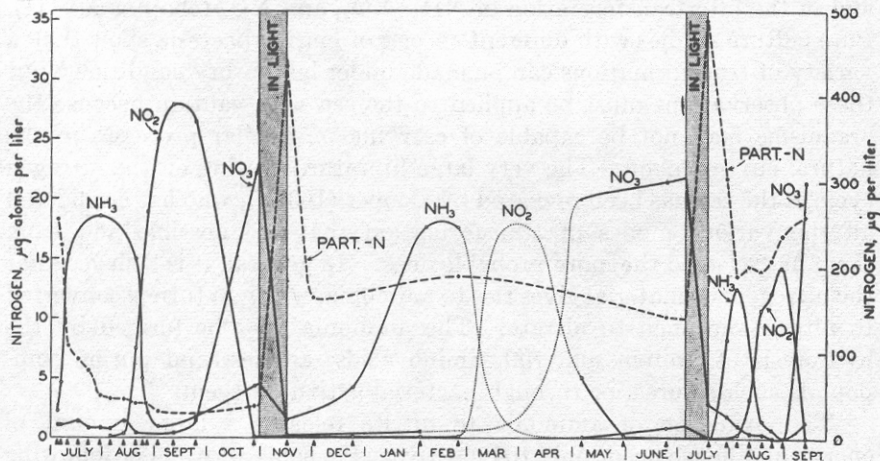

Fig. 61. Experiment on the utilization and regeneration of nitrate. When medium was placed in light, it was innoculated with diatoms. Data from von Brand, Rakestraw, and Renn, 1939.

and the fact that the water was enriched with organic material. It may also account for the fact that the NH_3 and NO_2 reached relatively high values (the same as the NO_3), and that during the regeneration the stages of production of NH_3, NO_2, and NO_3 were clearly defined (cf. figs. 57 and 58). Furthermore, it is interesting to note the great increase in the amount of nitrogen present as particulate material that was apparently resistant to the action of the bacteria present. At the end of the experiment, approximately 50 per cent of the nitrogen was in this form. Such a "waste" of nitrogen does not take place in the sea. It is also of interest to note that diatoms would flourish if the medium were placed in the light when either NH_3 or NO_2 were abundant and before the NO_3 had been produced. This supports the theory that marine plants can use any of these inorganic forms of nitrogen equally well.

NITROGEN CYCLE IN THE SEA. The chemically bound nitrogen in sea water is known to occur in living organisms, in dissolved and particulate material of organic origin, and as ammonia, nitrite, and nitrate.

The quantities present in these various forms vary from place to place, and in the upper levels may undergo seasonal changes. Much work has been done on the nitrogen cycle in the sea to determine the forms of nitrogen that can be used by the plants and the agencies which return the organic nitrogen to inorganic forms. In the surface layers, prior to the vegetative season, the most abundant inorganic form of nitrogen is nitrate, and in deeper water, where nitrite and ammonia are negligible, this is always the case.

Bacteria play important roles in the mineralization of organic nitrogen by acting upon detrital material, excreta, and dissolved organic matter, and in the intertransformation of NH_3, NO_2, and NO_3 (chapter XVIII). Pure culture studies with different species of marine bacteria show that a variety of transformations can be made under laboratory conditions, but these observations must be applied to the sea with caution because the organisms may not be capable of carrying on similar processes in the natural environment. The very large literature bearing on the nitrogen cycle in the sea has been reviewed by Cooper (1937b), who has considered all the various modes of transformation that are possible and from them has selected the more probable ones. In general, it is believed that the nitrogenous material gives rise to ammonia, which in turn is converted to nitrite and then to nitrate. The ammonia may be formed by the hydrolysis of protein material, amino acids, amines, and purine compounds such as urea, or through bacterial action on them.

The oxidation of ammonia to nitrite releases a large amount of energy and hence needs only to be activated in some way. The following agencies have been suggested:

1. Photochemical oxidation induced by direct sunlight. This reaction was first observed in sea water by ZoBell (1933), but, as pointed out by Cooper, can be effective only within the upper meter or so of water, owing to the rapid absorption of the shorter wave lengths that activate the reaction.

2. Chemical oxidation by the free oxygen in the water in the presence of surface catalysts. This reaction is of unknown significance.

3. Bacterial oxidation. Nitrifying bacteria are present in bottom sediments, and forms isolated by ZoBell (1935b) converted ammonia to nitrite. However, the conversion occurred at a much higher oxidation-reduction potential than is ordinarily found in the sediments. Studies of the decomposition of marine plankton *in vitro* show a conversion of ammonia to nitrite, but no nitrifying bacteria could be isolated (von Brand, Rakestraw, and Renn, 1937). Nonetheless, the fact that nitrifying bacteria cannot be readily detected in sea water is not definite proof of their absence. It is well known that many marine bacteria are difficult to culture, and development of new techniques may establish their presence. Carey (1938) has shown that they can be isolated from

water rich in plankton.   The presence of nitrite, which can sometimes be detected near the sea bottom, as in the English Channel in certain seasons, may indicate either oxidation of ammonia or reduction of nitrate. Although it has not been established, bacteria are probably the most important agency in the oxidation of ammonia to nitrite.

Oxidation of nitrite to nitrate also releases energy, and, as in the oxidation of ammonia, purely chemical or photochemical processes may be important.   Bacteria capable of making the transformation are abundant in sediments, but they are difficult to isolate from the water column.   Development of suitable techniques may also clarify this problem.   Cooper has pointed out that in sea water saturated with oxygen the nitrate in equilibrium with nitrite will be of a tremendously greater order of magnitude. Hence, the detection of nitrite in the water column may indicate active production of this substance, which is present only as a transitional stage in the regeneration of nitrate.   Brandt's hypothesis (p. 768) was based on the discovery of marine bacteria which under laboratory conditions were capable of denitrification.   However, it is now considered that under the conditions

Fig. 62.   Annual cycle in the phosphate content of the surface waters at Friday Harbor, Washington, and the monthly N/P ratios.

prevailing in the sea there is little or no loss of fixed nitrogen, although it has been shown that reduction of NO_3 to NO_2 may occur.   This reduction may also be carried out by diatoms, as has been observed in pure-culture experiments (Zobell, 1935a).

ORGANIC PHOSPHORUS AND SEASONAL VARIATIONS IN PHOSPHATE. For certain coastal areas, sufficient data exist to show the nature of the seasonal variations in phosphate.   Friday Harbor, the English Channel, and the Gulf of Maine have been selected as examples.

In fig. 62 are presented the averages based on about four years' observations of the monthly mean values for PO_4-P at Friday Harbor (Phifer and Thompson, 1937).   Highest values occur during the winter, and lowest values during the summer season, when phytoplankton growth has been great.   The monthly ratios of N:P are somewhat lower than the normal ratio proposed by Cooper, and their variability during the course of the year indicates that proportionally more nitrate than phosphate is utilized.   Neither of these substances can be considered as limiting the amount of phytoplankton produced at this locality. Phosphate data from the English Channel (Cooper, 1938b) for the period November, 1930, to January, 1932, are presented in fig. 63 as
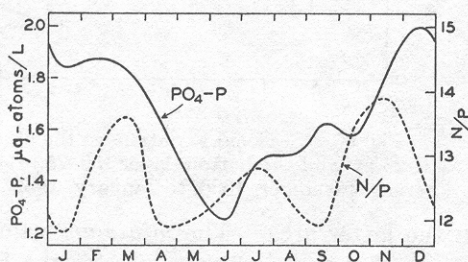
PO_4-P. In this shallow region there is never very much difference between the quantities in the surface and in the bottom layers. The amount of phosphate in the English Channel is much less than at Friday Harbor, although the difference between maxima and minima are of the same order, 0.5 μg-atoms/L in the former, and about 0.75 μg-atoms/L
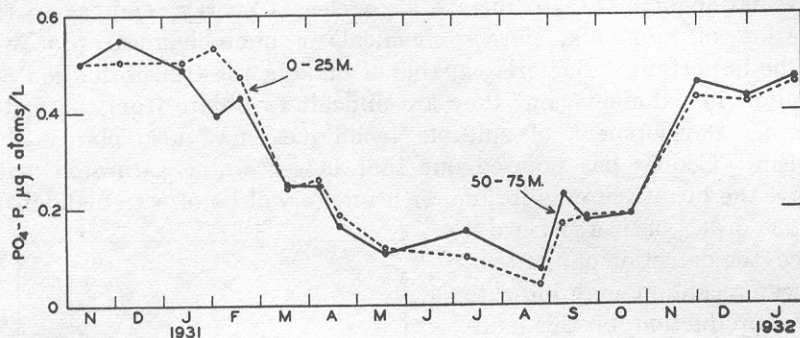

Fig. 63. Seasonal variations in the phosphate content of the surface layer (0–25 m) and the bottom layer (50–75 m) in the English Channel during the period November, 1930, to January, 1932.

in the latter area. The *minimum* values for San Juan Channel are in excess of the *maximum* values for the English Channel. Similar conditions hold for the nitrate (p. 252).

Cooper (1938b) has assembled phosphate data for the English Channel covering a period of eighteen years. In fig. 64 are entered the winter

Fig. 64. Winter maxima for phosphate in the English Channel for the period 1921–1938.

maxima for the average PO_4-P content of the water column near Plymouth. As the phosphate content of the water during the winter is a measure of potential production for the following spring and summer, his data indicate a drop in fertility after 1929 or 1930. The changes are considered to be associated with the circluation, which may undergo random or periodic fluctuations.

In the preceding discussion, emphasis has been placed on the cyclic nature of the seasonal variations, and it is obvious that the conditions in any area may not repeat themselves if disturbances, such as shifts in the circulation, bring about changes.

The seasonal variations in the PO_4-P and in the various organic phosphorus fractions in the Gulf of Maine have been studied by Redfield, Smith, and Ketchum (1937). During one year, five series of samples were collected at various depths between the surface and the bottom. These

samples were analyzed for PO_4-P, dissolved organic-P, and particulate organic-P. The results are summarized in table 54. The variations in total phosphorus during the year are ascribed to the fact that, although collections were made at the same locality, the circulation (advection) brought in water of different character. Table 54 shows that the particulate phosphorus never represents more than about 10 per cent of the total, but that the dissolved organic phosphorus sometimes occurs in relatively large amounts, in the upper 60 m approaching 50 per cent of the PO_4-P.

TABLE 54

SEASONAL VARIATIONS IN PHOSPHORUS DISTRIBUTION
IN THE GULF OF MAINE

Form of phosphorus	Interval of depth, meters	μg-atoms/L of phosphorus				
		May 18, 1935	Aug. 20, 1935	Nov. 8, 1935	Feb. 26, 1936	May 14, 1936
Phosphate	0–60	0.60	0.68	0.65	1.03	0.64
	60–120	1.11	0.91	1.08	1.02	1.25
	120–180	1.31	1.22	1.25	1.11	1.51
	180–240	1.61	1.39	1.22	1.51	1.60
Dissolved organic	0–60	0.08	0.34	0.29	0.07	0.14
	60–120	0.02	0.29	0.31	0.14	0.36
	120–180	0.01	0.17	0.29	0.17	0.15
	180–240	0.00	0.20	0.37	0.03	0.10
Particulate organic	0–60	0.15	0.10	0.10	0.05	0.12
	60–120	0.06	0.05	0.05	0.05	0.07
	120–180	0.04	0.03	0.08	0.03	0.02
	180–240	0.04	0.03	0.08	0.04	0.06
Total (Average for whole water column)	0–240	1.26	1.36	1.44	1.31	1.51

Earlier work on organic phosphorus in the sea has been summarized by Cooper (1937a), who also reports observations from the English Channel. Cooper points out that many determinations of the total "organic phosphorus" (both particulate and dissolved) probably include arsenite-arsenic that has been oxidized to arsenate when the organic matter was destroyed and that has not been reduced again. Arsenate will give the same reaction as phosphate in the colorimetric estimation, and, because the arsenic present as arsenite will not affect the inorganic phosphate analyses, the determination of "organic phosphorus" will be too high by about 0.2 μg-atoms/L (the concentration of arsenic). In the determinations in the Gulf of Maine this source of error was

eliminated. The "organic phosphorus," uncorrected for arsenic, averages about 0.4 μg-atoms/L (Cooper, 1937a). If reduced by one half to eliminate the effect of arsenic. this value corresponds to the average for the Gulf of Maine.

The maximum values reported by Redfield *et al* in the Gulf of Maine for particulate and dissolved organic phosphorus are

<div style="text-align:center">

Particulate P: 0.21 μg-atoms/L.

Dissolved organic P: 0.58 μg-atoms/L.

</div>

If multiplied by 16, the ratio of N:P in organisms, the corresponding values of particulate and dissolved organic nitrogen would be 3.4 and 9.3 μg-atoms/L respectively, which agree with determinations of nitrogen in the corresponding fractions (p. 254).

PHOSPHORUS CYCLE IN THE SEA. The cycle of phosphorus in the sea is rather similar to that of nitrogen except that only one inorganic form, phosphate, is known to occur. As shown above, phosphorus can be found in organisms, in particulate and dissolved organic compounds, and as phosphate. Probably only the phosphate is utilized by plants, and the dissolved organic fraction, which can originate as a metabolic product and from excreta, and the decomposition of organic material must be intermediate stages in the regeneration of phosphate. The roles that bacteria play are not yet known.

Studies of the decomposition of plankton material *in vitro* have led to some interesting results. Cooper (1935) added zooplankton and phytoplankton material of known phosphorus content to sea water and determined the rate at which the PO_4-P was formed. The PO_4 appeared more rapidly in the zooplankton samples than in the diatom material. Furthermore, the PO_4 produced in the zooplankton samples was in excess of that originally present as PO_4 plus that added in the particulate material. This excess was formed from dissolved organic phosphorus originally present in the water. The PO_4 in the diatom experiments never rose to the level of the original PO_4 plus that added, even after an interval of about five months. The initial rate of appearance of PO_4 was rapid, and in the zooplankton experiments the transformation was nearly complete in about two weeks. The difference in behavior of the plant and animal material cannot yet be accounted for. Seiwell and Seiwell (1938) found that zooplankton decomposition at 22° to 25°C (probably higher than the temperature of Cooper's experiments) was such that the formation of PO_4 was most rapid during the first day or two after death. This stage was often followed by a period when the rate of utilization of PO_4 by microorganisms in the experiments exceeded that of formation. On the basis of these experiments it is sometimes considered that the PO_4 must be regenerated more rapidly than the NO_3. However, field evidence offers little support for this theory. Examina-

tion of figures illustrating the seasonal variation shows that the minima and maxima in NO_3 and PO_4 occur in the same months, which would indicate that the relative rates of utilization and regeneration are about the same. Furthermore, estimates of plankton production in the English Channel based on the drop in PO_4 and NO_3 from winter maxima to summer minima (Cooper, 1938b) yield approximately the same results.

Dec. 4, 1930, to Aug. 26, 1931: Drop in NO_3-N = 6.3 μg-atoms/L.
March 23, 1931, to May 18, 1931: Drop in PO_4-P = 0.46 μg-atoms/L.

If these are utilized in the proportion of 16:1, the NO_3-N equivalent to the PO_4-P would be 7.4 μg-atoms/L. As only a small fraction of these amounts are ever present in living organisms, the water must contain an abundance of detrital or dissolved substances available for regeneration. If the rate of regeneration of PO_4 were quicker than that for NO_3, it would be expected that the drop in PO_4 would be much smaller. Although nothing is yet known concerning the absolute rates of regeneration in the sea, at least there is no evidence that their relative rates are very different.

Redfield, Smith, and Ketchum (1937), on the basis of the material summarized in table 54, have calculated the manner in which the various phosphorus compounds vary in the different layers, assuming (1) that all utilization of phosphate takes place in the upper 60 m, (2) that all downward transport of phosphorus is due to the settling of organisms and particulate material, and (3) that the upward transport is all due to eddy dif-

Fig. 65. Annual cycle in the silicate content of the surface waters at Friday Harbor, Washington.

fusion. From their examination it was concluded that decomposition and regeneration took place throughout the column of about 240 m of water.
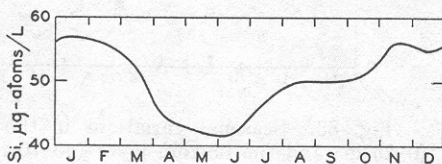
SEASONAL VARIATION IN SILICATE. Observations on the seasonal cycle in silicate-silicon have been carried out in many localities, of which Friday Harbor and the English Channel have been selected as examples. The data presented are comparable to those given for NO_3-N and PO_4-P. Fig. 65 shows the average monthly values for Friday Harbor based on more than four years' observations. The highest values occur during the winter and the lowest values during the early summer. The range in silicon is 15 μg-atoms/L. The ranges in SiO_3-Si, NO_3-N, and PO_4-P are in the proportions of 20:14.7:1. Data for the English Channel (Cooper, 1933) are shown in fig. 66. It will be noted that the concentration of silicon in the English Channel is much lower than it is at Friday Harbor, being in general only about $\frac{1}{25}$ as great. The range in silicon

during 1931 was about 3.5 μg-atoms/L, and the ratios of the ranges of SiO_3-Si, NO_3-N, and PO_4-P are 7.6:13.7:1. The ratios of utilization of NO_3 and PO_4 in the two areas are in reasonably good agreement, but there is a marked difference in the amount of silicon withdrawn. Whether or not this difference is associated with the character of the plankton or the sequence of plankton development in the two areas is not known. The seasonal cycle in the SiO_3 distribution in Monterey Bay was presented in fig. 56.
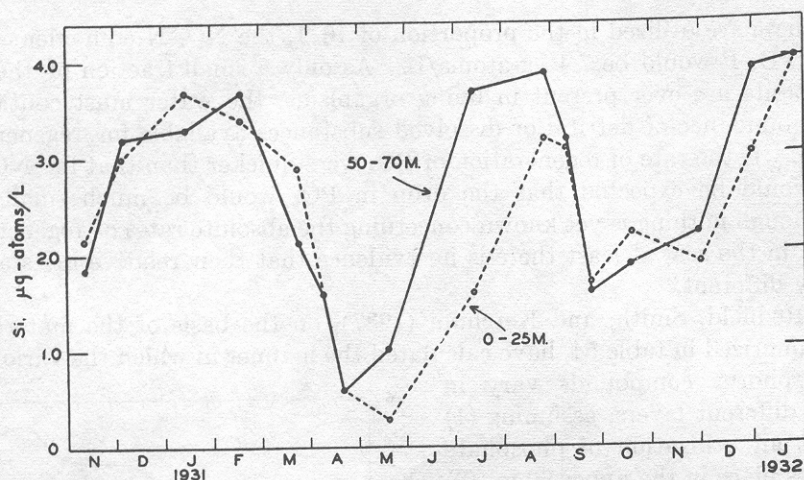

Fig. 66. Seasonal variations in the silicate content of the surface layer (0–25 m) and the bottom layer (50–70 m) in the English Channel during the period November, 1930 to January, 1932.

A factor that may complicate the seasonal changes in the silicon concentration in nearshore areas is the amount of siliceous material carried in by river waters, which is generally several times greater than that found in sea water; dilution will therefore tend to raise the concentration of silicate (Hutchinson, 1928).

THE SILICON CYCLE IN THE SEA. The depletion of the silicon in the surface layers is the result of biological activity and the sinking of the organisms or of their skeletal remains. The silicon removed from the water by diatoms or other organisms may return to solution after the death of the organism or may be deposited on the sea bottom. Unlike their roles in the cycles of nitrogen and phosphorus, bacteria are probably not directly involved in the re-solution of silicon from skeletal material. The skeletal material that sinks to the bottom forms either a temporary or permanent constituent of the sediments. Siliceous sediments are found in higher latitudes where the bottom material contains a very large proportion of diatom frustules, while in other regions radiolarian skeletons make up a large part of the sediment (chapter XX).

In the English Channel the silicon distribution is more erratic than that of PO_4 and of NO_3, and there may be large differences in the amounts at various levels. High values often occur near the surface and immediately over the bottom. The high surface values are ascribed to the effects of river water, the high bottom values to the re-solution of skeletal material that has settled there. The accumulation of dissolved silicates at a marked thermocline is also evidence of re-solution of slowly settling debris.

Estimates of plankton production in the English Channel based on the difference between the winter maxima and summer minima in PO_4-P, NO_3-N, and SiO_3-Si (Cooper 1933, 1938b) yield values from the SiO_3 data which are approximately $\frac{1}{15}$ of those obtained from the other elements. Cooper has attributed the smaller value to the rapidity with which the silicon passes through its cycle. The difference in the amount of silicon utilized in the English Channel and at Friday Harbor was noted above, and the fact that the concentration is reduced in the English Channel to a very low level may indicate that in that locality it does influence the production of diatoms.

King and Davidson (1933) found that the quantity of SiO_3-Si in solution affected the growth of diatoms in laboratory cultures. They also followed the changes in dissolved silicon after the death of the diatoms and found that complete solution took place in about five months. Marine phytoplankton were similarly studied, and it was found that samples which were boiled dissolved more slowly than those unboiled. The authors suggest the possible existence of an enzyme that hastens solution.

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