Oceanography

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PHILIP RICHARDSON

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Preface

The International Oceanographic Congress was a great day for oceanography. Some of us who attended it had been scientific sailors since we were very young. We could not have imagined in those days that we would meet one day in a great assembly with representatives from two thirds of all the earth's nations.

It was fitting that the Congress should be held in the home of the United Nations, for the marine sciences are peculiarly international. Not only can scientists of every continent and every country contribute to knowledge of the seas, but it is also necessary that they do so if our understanding is to increase.

From another point of view also, it was appropriate that those who are concerned with learning about the oceans, which are the property of no man and no nation but the heritage of every man and every nation, should meet in a building that belongs to no nation but to all mankind. By the ironies of science in our terrible century, the very existence of our human species is threatened while at the same time populations everywhere are exploding in size. No one knows how to predict or control what will happen to human society. We do know we must learn to govern our planet, to accept rationally and use wisely the planetary home in which all men are imprisoned. A first step in planetary government might well be the development of a wise and far-seeing international government of the oceans. But such governments depend on understanding. Oceanographers have a grave responsibility to the United Nations to achieve the understanding on which an international government of the oceans can be based.

Just as the United Nations is the meeting place for all the nations, the science of the sea is a meeting place for all the sciences. There are several definitions of oceanography, or oceanology, as many of my friends prefer to call it. Some say it is not a science at all, others that oceanography is what oceanographers do, or simply the science that is done at sea. I have had some success in defining it by pointing out that oceanographers are at heart just sailors who use big words. This is rapidly becoming an obsolete definition, because increasing numbers of young people who know a great deal about physics or biochemistry or quantum mechanics or microbial genetics or applied mathematics are becoming interested in one or another problem of the oceans. But for this very reason, oceanography is now, more than ever, a meeting place for all the sciences. Much of the fun of it, the sheer excitement of oceanography, arises when people of different backgrounds talk together about common problems, problems in which the ideas and knowledge of biologists, geologists, chemists, physicists, mathematicians, and engineers must be combined if a solution is to be found.

The Committee on Arrangements had this excitement in mind when they planned the Congress. On each day, in the morning lectures, published in this volume, and in the afternoon seminars, an attempt was made to emphasize the interrelationships between the scientific disciplines underlying oceanography, and thus to insure that biologists and chemists, geologists, and hydrodynamicists, would talk to each other. The results were not all we had hoped; there was in fact a certain amount of confusion. We should have expected this, if we had remembered the first rule of scientific progress, which is that the best research is accomplished by people who do not know very much about what they are doing.

The papers in this volume are not a summary of all existing knowledge about the oceans. Instead they are focused on certain broad problems that have recently been attacked with a new impetus. Nothing under the sun is completely new, and each of these problems has been written and talked about for many years. But during the last few years, new instruments, new techniques, and, above all, new people have combined in a vigorous new approach to these old problems. This new approach is characterized by the coordinated application of recent advances in basic sciences and by the careful formulation of questions.

The most striking common characteristic of the twelve hundred people who attended the Congress was youthfulness. Their average age was certainly under forty. This of course, reflected the fact that our science is a young one. Many of us in the pre-war generation of oceanographers felt completely outdated by the better-educated, brighter-eyed, and sharper-minded members of the new post-war generation. But we were proud to find how full our science is of uninhibited young people, full of new men with new ideas and new skills for attacking and solving the problems of the sea.

In my opening address to the Congress, I had the temerity to offer these young people three pieces of advice: (1) to ask questions of the ocean; (2) to think no small thoughts about their work; (3) to fan the flames of controversy.

Every science worthy of the name progresses, once it has passed the pioneering stage, by asking the right questions of nature. Indeed, ninety per cent of a scientific result has been achieved when an answerable question has been properly formulated. In the past we oceanographers have known so little about the oceans that we have had to depend pretty largely on blind exploration and random discovery. But I am convinced that we have now grown up intellectually—grown up to the point where the next great steps ahead will come from deliberate attempts to answer properly formulated questions and to test carefully conceived hypotheses. Much progress will come, especially in biology, from controlled experiments in the laboratory. But for many problems the sea itself must be used as a laboratory, and even though we cannot make a controlled experiment in the oceans we should be able, by carefully choosing the right conditions, to answer well-thought-out questions. An example is one of the problems to be attacked by the series of expeditions to the Indian Ocean proposed by the Special Committee on Oceanic Research—the problem of the magnitude and time scale of the changes in wind-driven currents brought about by changing winds. The Indian Ocean, with its two wind systems alternating seasonally, would appear to be an ideal laboratory to study this problem

Although our science is a small one, and our ocean is only a film of water on a small planet, yet we should not be too modest about what we are doing. The marine sciences are concerned with some of the most profound questions of mankind, questions that men began to ask when they first looked upward at the stars and inward toward themselves. We have good reason to believe that the earth is nearly as old as the Milky Way galaxy, and the records of the past preserved on earth, if we could only learn to read them, are the best archive available to us of the history of the galaxy. Most of these records are locked in the sediments and rocks beneath the sea, in the sea water itself, and in the atmosphere above the waters. Even more significant are the problems of the origin and history of living things, and here again we must turn to the oceans for many of our answers.

During World War II one of my friends in Washington had a cardboard sign crudely lettered in red over his desk. It said, "Fan the flames of controversy." No motto could be more appropriate for a scientist, for science progresses not only through the thinking of individuals but also through individuals talking and thinking together, through the mutual thinking and free interplay of several minds stimulated by a common problem and quickened by each other. This is especially true of oceanography, in which the answers to many questions require the application of more kinds of knowledge than can be held in the mind of one man. The best mutual thinking is done not when our minds are cooled by platitudinous politeness, but when they are warmed by a hot discussion.

One of the lasting values of the International Oceanographic Congress was that a number of bonfires of controversy were lighted and some of them were fanned to a bright flame.

Roger Revelle

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I. History of the Oceans

Shape and Structure of Ocean Basins*

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Shape of Ocean Basins†

Continents and Oceans

WE shall take as a starting point the familiar idea that the continents are blocks of low-density sialic rock, remarkably uniform in thickness and other properties, which are in isostatic or floating equilibrium on a heavier substratum, the sima. These blocks cover about 35% of the earth's surface. The peculiar shapes and the distribution of the blocks have given rise to many speculations about their origin and their permanence in size, shape, and relative position. Such speculations obviously relate directly to the shape, structure, and history of ocean basins.

We shall assume familiarity with general information about the shapes of the ocean basins and the distribution of oceans on the globe. For example, the earth's surface may be divided into a Pacific or "water hemisphere," which is about 89% ocean, and a "land hemisphere," which is only about 53% ocean. The pole of the land hemisphere is at about 47°N Lat, 2°W Long (Dietrich, 1957, p. 1). We also assume knowledge of the fact, much used by proponents of continental drift, that if the Americas should be displaced eastward to close up the Atlantic Ocean, their boundary would neatly fit the Mid-Atlantic Ridge at the halfway mark, and then the boundary of Europe and Africa. In this connection the reconstructions of Köppen and Wegener, Du Toit, and others, in which all of the land areas are fitted neatly together, may be called to mind.

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† This section by Maurice Ewing.

Depth-Frequency Relation

We also take for granted acquaintance with the statistics about area in relation to depth, as shown in the hypsographic and depth-frequency curves, e.g., Dietrich, 1957, p. 6 (Fig. 1). There are two predominant levels, one represented by a broad maximum of the frequency curve at about −4950 m (2700 fm) and the other by a sharper maximum at about +100 m (55 fm).

The lower level is of fundamental structural importance. From the depth-frequency curve we see that it represents the prevailing water depth in deep sea basins, which occupy about 45% of the total earth surface. It is the level for the typical oceanic column of mantle, crust, and sediment. Its actual depth below sea level depends simply on the amount of water in the oceans, but its elevation with respect to the mean elevation of the continental masses is a fundamental geophysical constant which is affected only in a secondary manner by the weight of water in the oceans.

The +100-m level represents the continental shelves, coastal

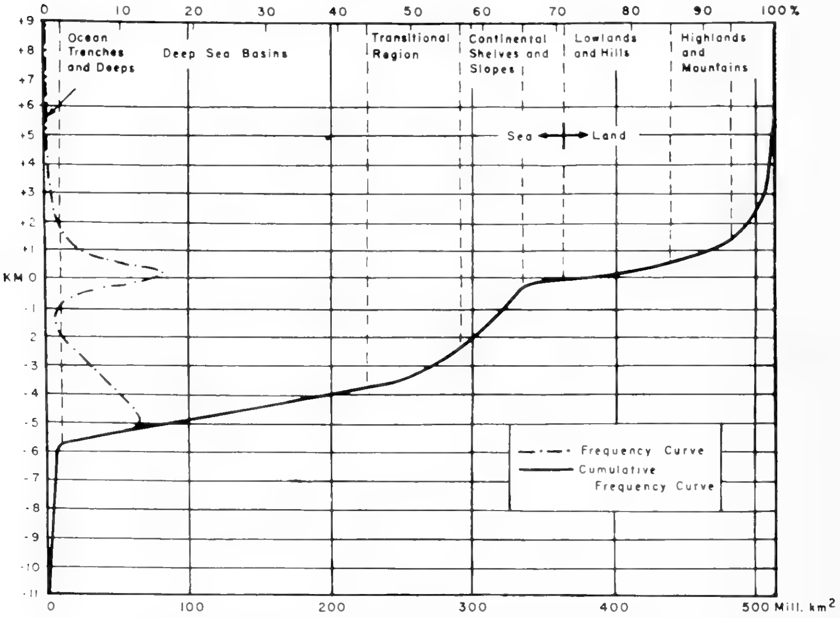

Fig. 1. Hypsographic and depth-frequency curves (after Dietrich, 1957).

plains, and continental lowlands. It results from subaerial erosion which effectively reduces the elevation of land surfaces and fills marginal seas, eventually to sea level. Its elevation above the floors of the ocean basins depends primarily on the volume of water in the oceans. Through the action of isostasy, however, the sea level influences the thickness of the continental crust. The +100-m level includes much of the shield area of the earth, and the fact that shield areas are generally so well adjusted to present sea level is strong evidence that the volume of sea water has been essentially constant for more than 500 million years. If we extend the +100-m level somewhat (to include regions of low hills up to 700 m), this level accounts for about 20% of the total earth surface.

Deep sea trenches account for 1 to 2% of the surface, and mountain chains and highlands for about 15%.

The remaining 18% includes depths from about 200 m to 3500 m, contains parts of the mid-ocean ridge system, but consists principally of the transition zone between continents and oceans—the continental borderlands including continental slopes and continental rises.

Continental Borderlands

There are many patterns of transition from continent to ocean, but the great majority of them can be put usefully into three classes (Fig. 2). In the first pattern, the sequence of form is shelf, slope, trench, ridge, and basin (westward from Peru). The second pattern differs in having a marginal sea and island arc between slope and trench (north from Venezuela). The third is represented by the sequence shelf, slope, rise, and basin (east from New Jersey).

Seismic refraction measurements have shown that in some instances the three patterns are structurally similar, apparent differences having arisen from burial by younger sediments (Drake *et al.*, 1959).

Mid-Oceanic Ridge System

The Mid-Oceanic Ridge system, typified by the Mid-Atlantic Ridge, is an important and extensive feature of the earth's crust

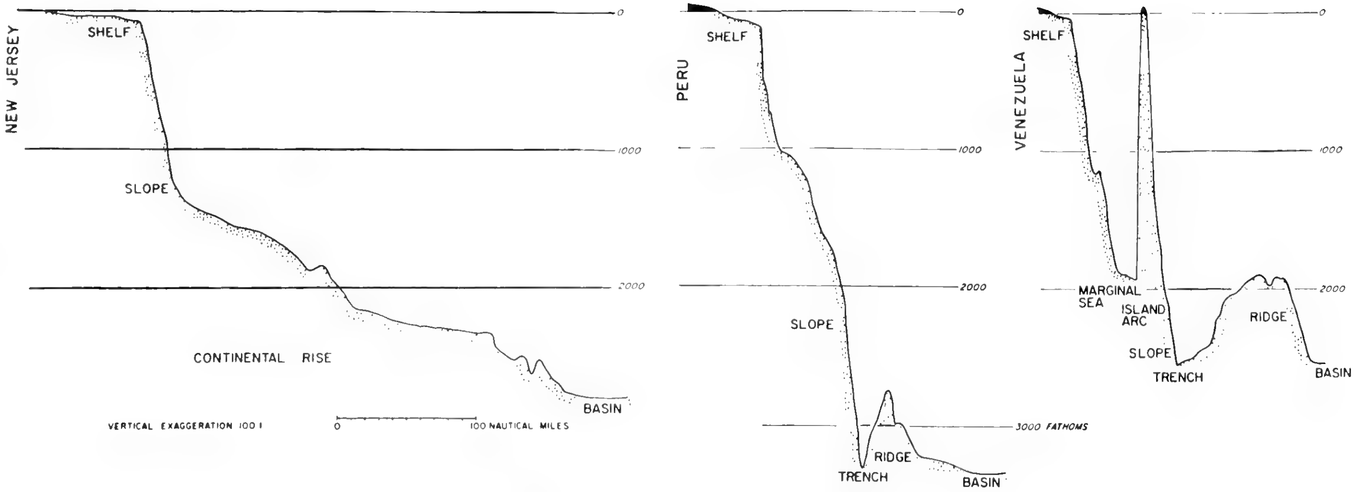

Fig. 2. Patterns of transition from continent to ocean.

which is not displayed in a clear fashion in the hypsographic curve. On a typical trans-Atlantic profile between New England and Spanish Sahara (Fig. 3), the Mid-Atlantic Ridge appears as an elevation about 1000 miles wide which reaches about 2 miles above the basin floor. It occupies approximately one-third of the whole Atlantic Ocean area, and, as has been shown recently, has an extension which occupies about the same fraction of the area of the Indian Ocean and then crosses the Pacific. Together with its extensions, it forms the Mid-Oceanic Ridge system about which the following facts have now been clearly established:

1. The Mid-Oceanic Ridge system is continuous and can be traced with certainty through a 40,000 mile world-encircling belt, which passes through the Atlantic, Indian, Pacific, and Arctic oceans, as shown in Fig. 4.
2. A deep, narrow median valley or trench, from 20 to 80 miles wide and ½ to 1½ miles deep, is a characteristic feature of the ridge through the Atlantic and Indian oceans. Apparently the valley is not conspicuous in the Pacific.
3. A seismic belt, in which all shocks are shallow focus, is continuous along the ridge and coincident with the median valley (insofar as the valley position is known).
4. The earthquake belt and an associated rift system extend into continental areas in several places.
5. In contrast to land mountain systems, this range of submarine mountains consists of a thin upper layer, with seismic velocities of about 4.5 to 5 km/sec, and a mass 30 to 40 km thick in which the velocity is about 7.3 km/sec.
6. The ridge shows a striking tendency to bisect the oceans through which it passes, if we grant that the southeast Pacific is an exception.

The demonstration that the Mid-Atlantic Ridge may really be extended, as a continuous tectonic and morphologic feature, throughout the world-circling pattern shown in Fig. 4, has been difficult, because many parts of the ocean are unsounded. Further, there are a number of oceanic ridges which are not a part of the system. Decisive evidence first came from the study of seismicity of the oceanic areas of the earth.

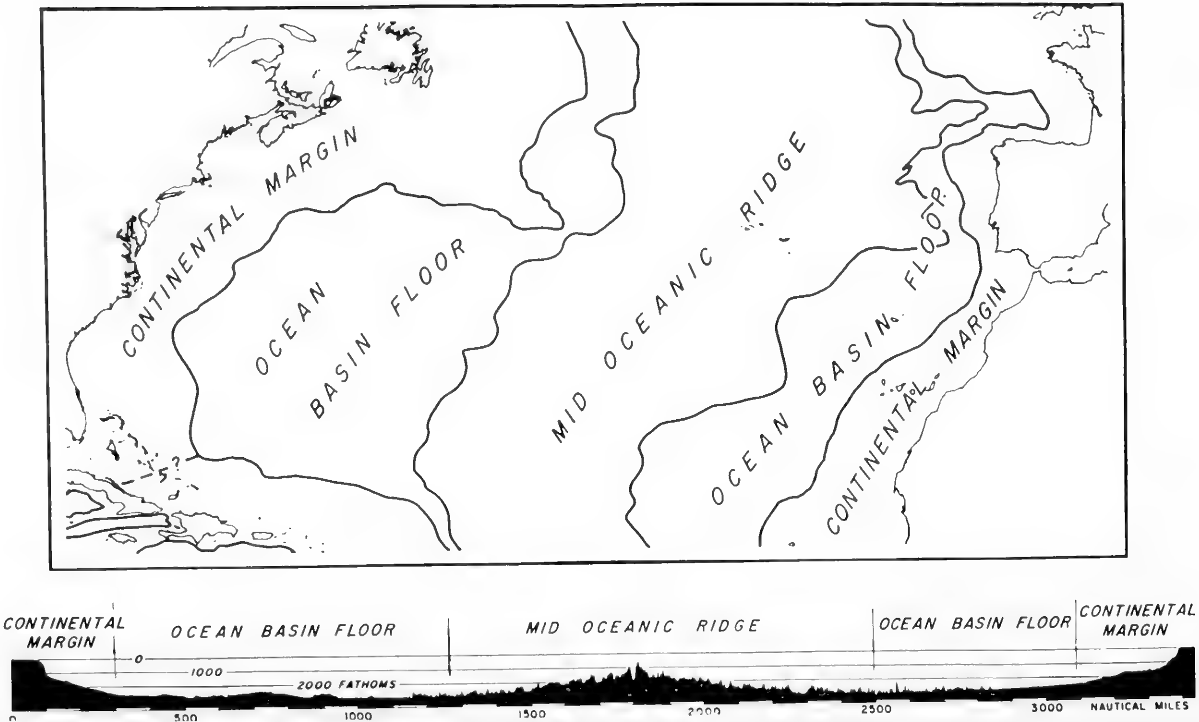

Fig. 3. Major morphologic divisions of the North Atlantic Ocean. The profile is a representative profile from New England to the Sahara Coast (Heezen, Tharp, and Ewing, 1959).

It has been known for about 70 years (Rudolph, 1887, 1895) that the Mid-Atlantic Ridge is a seismically active belt. Since the introduction of seismographs, epicenters have been located in increasing numbers and with gradually increasing accuracy. The seismicity of ocean areas has been discussed by various authors (Tams, 1922, 1927, 1928, 1931; Rajko and Linden, 1935; Mushketov, 1935; Heck, 1938; and Rothé, 1954). In their classic work *Seismicity of the Earth* (1949) Gutenberg and Richter discussed three oceanic active earthquake belts, the Arctic Belt, the Atlantic Belt, and the Indian Ocean Belt, and showed a strong correlation of seismicity with mid-ocean rises. But even at that time submarine topography was imperfectly known, particularly in the southern hemisphere, where sensitive seismographs also were few. The number of shocks that could be located was small and the precision of location was poor, so the continuity, and even the trend, of the seismic belts was obscure in several critical areas, e.g., between the South Sandwich Islands and Africa. During recent years epicenter location has greatly improved, so that the continuity, position, and linear character of a belt of shallow-focus earthquakes following the line shown in Fig. 4 is beyond doubt.

On all expeditions of Columbia University's Research Vessel *Vema*, the tracks have been planned to permit crossing the critical parts of the ridge as many times as possible. On every crossing the ridge has been found where it was expected, with its median rift accurately following the mid-oceanic earthquake belt.

This has been found true so many times that now we may say with certainty that the broad (up to 1000 miles wide) ridge can be traced by following the narrow median earthquake epicenter belt. The width of the belt is not appreciably greater than that attributable to epicenter location uncertainty.

Recently *Vema* has crossed the earthquake belt in many places where the existence of a ridge had never been considered as a possibility by most geologists, but in every case the ridge and rift were found (Ewing and Heezen, 1960).

The earthquake belt extends into continental areas in several places, permitting a more detailed examination of many of the

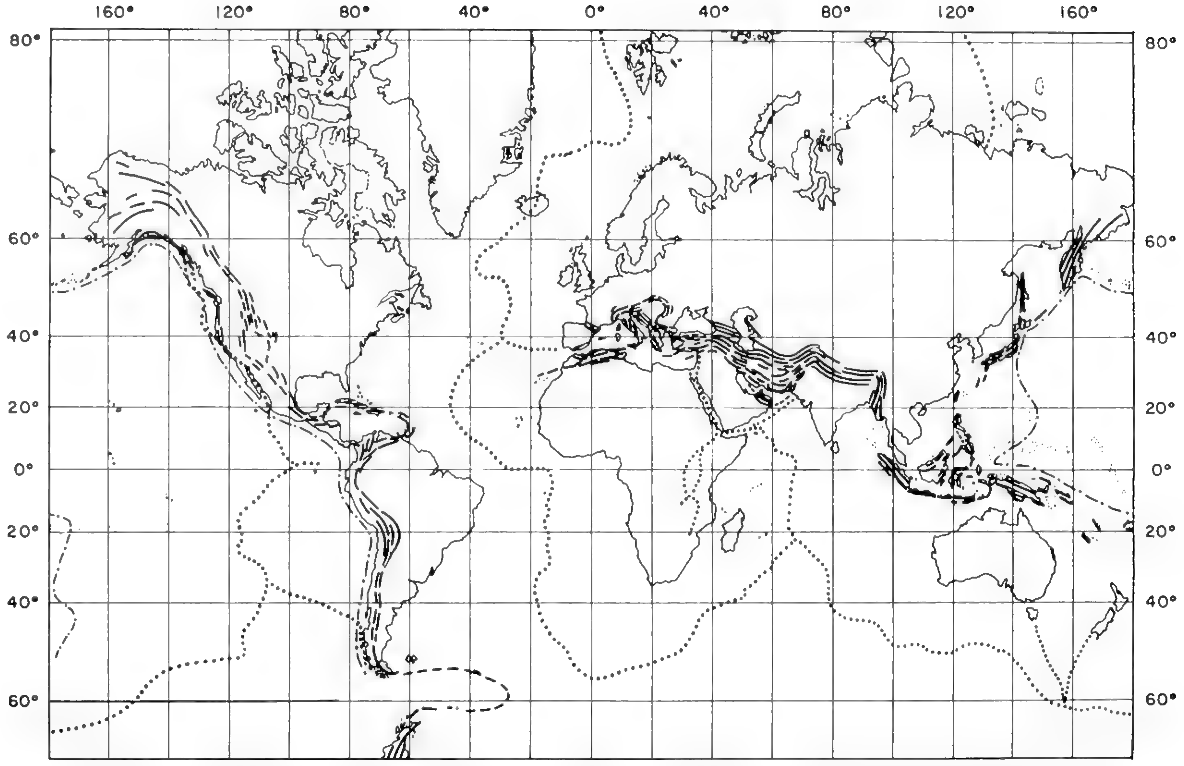

Fig. 4. The Mid-Oceanic Ridge System and the major orogenic belts of the earth (adapted from Umbgrove, 1947).

associated structural features than in the oceanic portions. These landward extensions, as shown in Fig. 4, include one from the Carlsberg Ridge through the Gulf of Aden and into the East African Rift Valleys; one from Easter Island into southern Chile; one from Easter Island into the Gulf of California; one from the vicinity of Spitzbergen into Siberia in the vicinity of the Verkhoyansk Mountains, and apparently three from the vicinity of Macquarie Island into Tasmania, New Zealand, and the Ross Sea, respectively. These landward extensions may be interpreted as zones in which the crust has failed under tensional forces, accompanied by the extrusion of basic and ultrabasic lavas.

There are a few areas in which no rift has been found (Dietrich, 1959) possibly owing to filling by sediments or lavas, and there are some indications that in the eastern Pacific the morphology of the ridge may be different from that found elsewhere but, if so, the boundary line between the two types is yet to be determined. It is possible that in some areas there is a narrow median system of an echelon of rifts rather than a single continuous rift. The relations and contrasts between the seismic and aseismic ocean ridges are gradually being discovered. But even now it is apparent that the Mid-Oceanic Ridge system is a major morphologic element of the ocean basins which also offers direct information about fundamental tectonic processes.

It has been established that the Mid-Oceanic Ridge system, of which the Mid-Atlantic Ridge is the best known part, is a continuous, world-encircling system, about 40,000 miles long, which is characterized by a median rift and a coincident narrow belt of shallow-focus earthquakes. The significance of the differences in structure between the Mid-Atlantic Ridge and typical land mountain systems, and the significance of the striking tendency of the ridge to bisect the oceans will be discussed in the next sections.

Crustal Structure of Ocean Basins*

General Statement about Crust and Mantle

For the purpose of this paper the crust (or silicic crust) is

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* This section by Maurice Ewing.

considered as all the solid earth above the mantle, being separated from it by the Mohorovičić discontinuity. The crust extends to depths of 35 to 55 km below sea level under the continents, and to 10 to 12 km below sea level (4 to 6 km below the ocean floor) under the oceans.

There is a great discontinuity in the velocity of elastic waves, and probably also in composition, at the Mohorovičić discontinuity. Almost everywhere the uppermost part of the mantle is considered to be peridotite, with compressional (*P*) and shear (*S*) wave velocities of 8.1 and 4.6 km/sec, respectively. The continental crust, in many continental areas, has been divided into an upper and lower part, separated by the Conrad discontinuity. The upper part consists principally of granitic, volcanic, and sedimentary rocks, many of which have been strongly metamorphosed. Elastic body wave velocities in the upper part of the crust range up to 6.5 and 3.6 km/sec for *P* and *S*, respectively (Katz, 1955). The lower part of the crust, both under continents and under oceans, is believed to be basaltic rock, in which the seismic velocities are about 6.7 and 3.8 km/sec. Data for typical continental and oceanic crustal sections are given in Table I.

Crustal Section for Ocean Basins

In the earlier reports of seismic refraction results for oceanic crust, only water, sediment, and a crustal or "oceanic" layer were mentioned. But later, in many areas, an additional layer has been found between the oceanic layer and the sedimentary layer. The velocity in it is 4.5 to 5.5 km/sec, the average being about 5 km/sec. The average thickness of this layer is about 1–2 km. It is probably present in many areas where previously not reported, owing to masking of its refraction arrival by the sedimentary and oceanic layers.

The sedimentary column for typical basins in the Atlantic averages about 500 m, whereas in many parts of the Pacific the average is 300 m. This difference may be accounted for by the remoteness from land of large parts of the Pacific, the relative scarcity of rivers which bring large sediment loads, and by the presence of sediment traps (the deep-sea trenches which occur along a large part of the border of the Pacific).

TABLE I. Wave Velocity and Layer Thickness for Typical Continental and Oceanic Crustal and Upper Mantle Sections[a]

	Continental Crust			Oceanic Crust		
	P vel, km/sec	*S* vel, km/sec	Thickness, km	*P* vel, km/sec	*S* vel, km/sec	Thickness, km
Water	—	—	—	1.5	—	5
Sediments	0.3–5.5	0–3.2	0–16	1.5–2.5	—	0–1
Upper crust	6.2	3.5	10–30	4.5–5.5	2.6–3.2	1–2
Lower crust	6.7	3.8	20–30	6.7	3.8	3–5
Upper mantle	8.1–8.2	4.6–4.7	80–100	8.1–8.2	4.7	50
Low-velocity layer	—	4.2–4.3	80–100	—	4.3	150

[a] The section on "Mantle Structure of Ocean Basins," page 18, contains a fuller discussion of the data given here for the mantle.

The oceanic layer does not show systematic differences in thickness or composition from one ocean to another; but in all oceans for which we have data there are exceptional areas in which this layer deviates considerably from the normal, e.g., the mid-oceanic ridges, the island arcs and deep-sea trenches, and the continental borderlands.

A considerable quantity of data (largely unpublished) on seismic reflections in the oceans, for both vertical and wide angle reflection arrangements, has been gathered by the Lamont Geological Observatory staff. In a few areas there is found a good reflection whose depth agrees with that found for the oceanic layer by refraction measurements. There are usually one or more strong reflections from within the sedimentary layers. At the majority of stations the reflection from the oceanic layer is weak to undetectable (by the rather primitive methods used) in comparison with the reflection originating within the sedimentary column. There is need for continuing investigation of the structure of the layers above the oceanic layer and of the nature of their contact with it. For example, the investigation of these layers by drilling and coring is many-fold easier to accomplish and offers scientific rewards many-fold greater than the proposed investigation of the upper mantle by drilling—the so-called Mohole project.

Conversions of part of the *P* wave energy into *S*, at some point on the downward path of refracted rays, and reconversion at the corresponding point on the upward path, have been reported in several papers (Nafe and Drake, 1957; Ewing and Ewing, 1959a). The situation here is similar to that described for reflection studies, in that conversion more commonly occurs at some level above the oceanic layer than at its upper surface. Here again there is the possibility for increase and refinement of our knowledge about the superficial layers and their contact with the oceanic layer.

It is only very rarely that either the reflections or the conversions give positive information about the M (Mohorovičić) discontinuity. Our positive information about it comes principally from refraction measurements. Almost everywhere in the ocean basins, the M discontinuity, as judged by seismic refraction measurements, is a sharp, smooth boundary between rocks of the contrasting types listed in Table I. These rocks are usually taken to be basalt and peridotite. There are, however, exceptional areas in which the transition is not sharp, as described above. and in which the familiar rock types are not identifiable. These exceptional areas are the island arcs and deep sea trenches, the continental margins, and the Mid-Oceanic Ridge system.

Mid-Oceanic Ridge System

The Mid-Oceanic Ridge system affords an outstanding example of an extensive area in which the crustal structure differs widely from that typical of the ocean basins. The Ridge is up to 1000 miles wide and rises 1 to 2 miles above the floors of the basins which commonly occur symmetrically on both sides of it. From seismic refraction measurements (Ewing and Ewing, 1959a) we know that it is commonly capped by a rock layer 3 to 5 km thick in which the velocity of P waves is 4.5 to 5.5 km/sec, appropriate for volcanic rocks as in Fig. 5.

Beneath this cap, to a depth which probably ranges up to 35 to 40 km, is the main body of the ridge, with a compressional wave velocity of about 7.3 km/sec. It has been suggested (Ewing and Ewing, 1959a) that this velocity which is intermediate between those for typical oceanic crust and mantle, may represent a mixture of crustal and mantle rocks. The depth of 35 to 40 km, at which a velocity of 8.1 km/sec would be found, was estimated on the

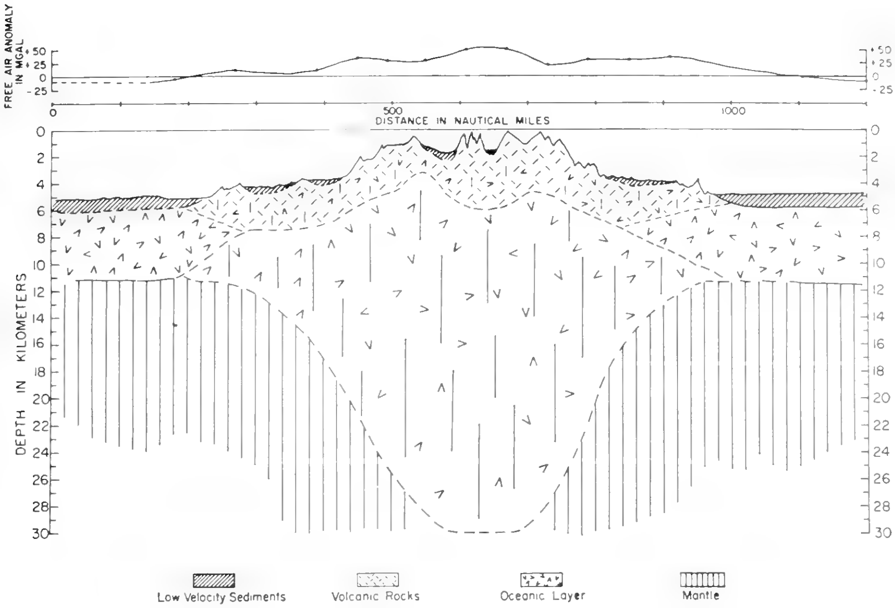

Fig. 5. Structure section across the Mid-Atlantic Ridge (Ewing and Ewing, 1959a).

assumption of isostasy. An interesting alternative suggestion about the appearance of a velocity of 7.3 km/sec so near the surface arises from noting that the linear extrapolation of the outer mantle velocity-depth curve of Fig. 7 to the surface gives also the velocity of 7.3 km/sec. In other words, the observed velocity pattern could conceivably arise from pulling or pushing the lithosphere aside and allowing material of the outer mantle to rise toward the surface.

A third view is that of Hess (1959), who suggests that the elevation of the ridge results from a phase change from peridotite to serpentine induced by the addition of water. This produces an increase of volume, evolution of heat, and a suitable decrease in elastic wave velocities. Additional measurements, like those of Birch (1960), are needed for appraisal of this suggestion.

Deep-sea trenches, island arcs, and marginal seas are associated features, which will be discussed together as a class of anomalous oceanic regions. The island arcs are chains of submarine mountains, commonly situated only a few hundred miles off shore from a continent and enclosing a marginal sea (e.g., the West Indian Island Arc and the Caribbean Sea). The mountain range may sometimes be found at the margin of the continent, (e.g., the Andes) or far out in the ocean (e.g., the Marianas), but in all cases the mountains consist largely of andesitic rocks. There is a parallel deep-sea trench, on the side toward the ocean, and there is seismic activity which usually includes foci at greater than normal depths. The deeper foci are systematically displaced toward the continent side of the arc. There are also significant gravity anomalies over the trenches.

Since the importance of turbidity currents in long-range transportation of deep-sea sediments has been recognized (Heezen and Ewing, 1952), it has been clear that deep-sea trenches were likely to become rapidly filled with sediments (Ewing and Heezen, 1955). This was to be expected provided rivers carrying large volumes of sediment were so located that no topographic barriers intervened to deny access to the turbidity currents. The presence of such filled trenches has been demonstrated by seismic refraction and by gravity measurements. For example, the Puerto Rico Trench is a structural feature which curves southward around the Lesser Antilles and continues through Barbados (Officer *et al.*, 1957). But the trench has disappeared as a topographic feature through being filled with sediments to a thickness of about 8 km, evidently from the Orinoco and the rivers of the Guianas. As additional examples of filled trenches, we may cite that just north of the islands Aruba, Curaçao, and Bonaire, (Hennion and Ewing, in preparation) and one in the Scotia Arc, from Staten Island and Burdwood Bank to the vicinity of South Georgia. Here also the sedimentary filling is about 8 km thick (Ewing and Ewing, 1959b). By way of contrast, the South Sandwich Trench is an excellent example, like many of those in the Pacific, of a trench which is not being rapidly filled owing to the lack of access of turbidity currents.

Marginal Seas

The marginal seas, such as the Caribbean and Scotia seas, have sometimes been described as oceanic regions which are partially enclosed by island arcs. The arcs possibly have originated through metamorphism and uplift of sediments, which were earlier collected in trenches and later incorporated into magma to form andesitic volcanic rocks. It has been found, by seismic refraction surveys, that the crust inside the Caribbean Sea is not of a single type, but that it varies widely between a typical oceanic type in the deeper areas to a pseudo-continental type in the enclosing ridge, as well as in many subsidiary ridges within (Officer *et al.*, 1959; Ewing *et al.*, 1960).

Continental Margins

The continental margins are a region which has been difficult to explore by means of seismic refraction measurements, owing to sharp topographic changes, plus a rapid transition in thickness (and usually in composition) of many of the layers concerned. Gravity measurements (Worzel and Shurbet, 1955) have shown that the transition is a sharp one in the regions studied. This conclusion is confirmed by numerous recent studies on the behavior of "crustal" Love and Rayleigh waves at continental margins. Refraction effects have been noted over the relevant period range, and strong attenuation occurs, for waves crossing the continental margins, in some parts of the period range. This is probably attributable to a strong, sharp contrast in the impedances of the wave guides responsible for the wave transmission (Oliver *et al.*, 1955).

Heat Flow

The flow of heat through the crust has been found to be about 1×10^{-6} cal cm^{-2} sec^{-1} for typical continental and oceanic areas, but is significantly higher for all areas sampled on the Mid-Oceanic Ridge system. Bullard *et al.* (1956), von Herzen (1959), Maxwell and von Herzen (1959), and E. C. Bullard and A. Day (personal communication) have reported significantly higher flux for the ridge both in the Atlantic and the Pacific. This important result is confirmed by measurements (not yet published) made on *Vema* in the Atlantic, Pacific, and Indian oceans.

Crustal Summary

There is a strong contrast between typical crustal sections for continents and for ocean basins. Of the ocean areas where anomalous crustal structure is found, particular attention is directed to the Mid-Oceanic Ridge system. In this region the lithological composition of the crust and the thermal flux through it suggest that matter and heat have been brought toward the surface on a large scale more recently than in other major divisions of the earth's surface.

Mantle Structure of Ocean Basins*

We have discussed the great difference between continental and oceanic areas in regard to crustal structure. It is necessary to know whether this difference extends into the upper mantle. If so, there are important implications about origin of the continents, possibility of continental drift, and most of the major tectonic problems.

Body Wave Studies

The transmission of earthquake body waves, of both compressional and shear types, through the earth has been the most fruitful means of investigation of the earth's interior. The ray paths and wave fronts in the mantle and core are shown in Fig. 6.

Information about upper mantle structure was formerly derived exclusively from travel times and amplitudes of body waves at epicentral distances less than 25°. It was therefore restricted to continental areas in which there were numerous earthquakes and also numerous and well-distributed seismographs, out to epicentral distances of about 25°. Compressional and shear wave velocities of about 8.1 and 4.5 km/sec for P and S, respectively, were generally found at shorter distances, but beyond 10° the interpretation of the arrivals became obscure. Between 13° and 20°, depending perhaps on the region investigated, Gutenberg (1948), Lehmann (1954), and others have shown that there is a large change in amplitude, some changes in wave character including

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* This section by Maurice Ewing and Mark Landisman.

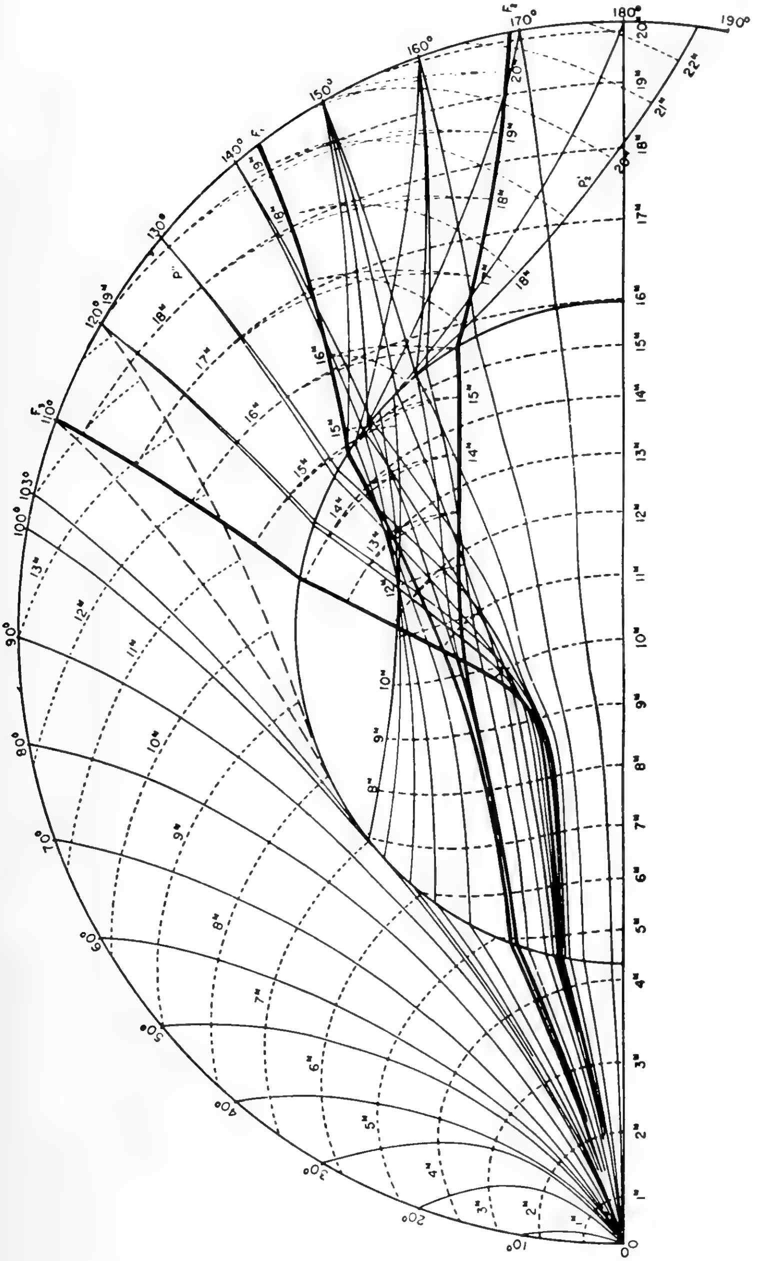


Fig. 6. Compressional (*P*) wave fronts and ray paths through the core and mantle for a surface focus earthquake (Gutenberg, 1951).

multiplicity of arrivals, and an increase in the apparent surface velocities to about 9 and 5 km/sec for *P* and *S*, respectively. Lehmann (1934, 1952, 1955) concluded that "there is likely to be a layer in which there is a decrease in the velocity of *S* waves." Gutenberg (1948) concluded from studies of more detailed data, that in Southern California there is a low-velocity layer at a depth of 80–100 km affecting both *P* and *S*. Gutenberg (1953) introduced a new method which made use of the fact that the velocities at the depth of an earthquake focus may be determined by the slope of the tangent of the travel time curve at the inflection point. Data from small epicentral distances were available for intermediate and deep earthquakes, but mainly for Japan alone. He reported that elastic wave velocities "show a clear decrease with depth with a minimum at a depth of roughly 100 km for longitudinal waves and 150 km for tranverse waves" and presented evidence for a strong increase of compressional and shear velocities below 200 km (see Fig. 7). This method was even more restricted in its areas of applicability than the earlier one, but it was the first capable of giving direct measures of velocity variation within a low-velocity zone. The previously used methods could only indicate such a layer by a "shadow zone" in which the data obtained seemed very poor, and by a delay between the travel-time curve for large distances, compared to that extrapolated from small distances.

Lehmann (1955) reported that in northeastern North America the near branch of the *S* travel-time curve extended to 14°. Contrasting this to the 5° limit which she had found in Europe, she inferred regional differences in upper mantle structure, and postulated that a "soft" layer, having reduced shear wave velocity, was somewhat deeper in northeastern North America than in Europe. However, Lehmann believed that no low-velocity channel exists for *P* since there is no delay between the near and far boundaries of the time curve, the small amplitude of *P* at distances less than 15° being explained by the straightness of the time curves. (Compare Fig. 7 for Gutenberg's results.)

Lehmann (1954) discussed the relation of Gutenberg's low-velocity zone to the strain rebound studies of Benioff (1954),

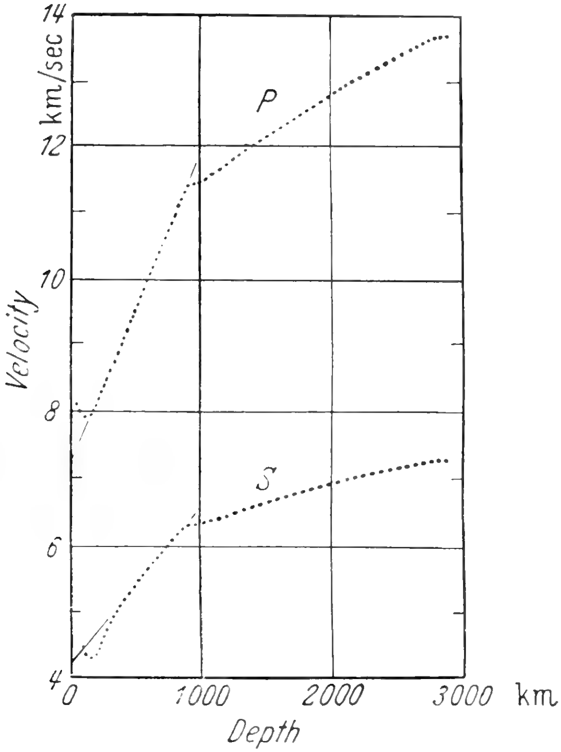


Fig. 7. Compressional (*P*) and shear (*S*) wave velocities in the earth (after Gutenberg, 1958).

particularly to results such as those shown in Fig. 8. The increase in compressional and shear velocities at a depth of about 200 km or slightly below was compared with the similar depth found by Benioff for the juncture of two systems of energy release for orogenic regions bordering continents (e.g., Kuriles and South America). On the basis of this comparison, Lehmann suggested that "the 200–300 km level thus represents a tectonic discontinuity which is apparently the lower boundary of the continents." Lehmann's more recent work (1959, 1960) has strengthened the concept of a sharp increase of *P* and *S* velocities at a depth of about 220 km below Europe and northeastern North America, which depth would mark the bottom of the low-velocity zone.

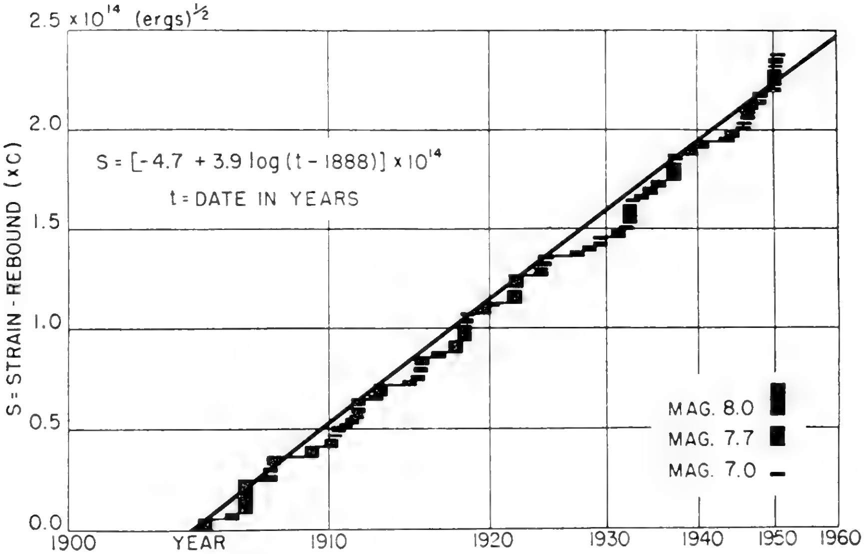


Fig. 8. Plot of strain-rebound, S in (ergs)$^{1/2}$, vs date, t in years, for a sequence of earthquakes with focal depths $h > 300$ km and magnitude $M \geq 7.0$ since 1905 (incomplete for magnitudes 7 to 7½ for 1905 to 1917). These shocks occur below the low-velocity region (after original by H. Benioff, from Gutenberg, 1959).

As will be seen from the results of surface wave dispersion, it now seems more likely that the lower boundary of the continents is at a lesser depth, roughly 100+ km, where these studies placed the lower boundary of the high-velocity, topmost mantle layer.

There is also the strong possibility that Benioff's and Gutenberg's results do not apply to normal mantle structure, since the data are inherently restricted to anomalous regions such as deep trenches and continental margins.

It seemed likely that, despite the variability of body wave results, a standard upper mantle structure for continental areas did exist, because the velocity-depth curves for depths greater than 400 km were well determined and in excellent agreement for many areas. But there seemed to be little possibility of making detailed upper mantle investigations of a significant number of representative continental areas to determine the standard continental structure, and there was no possibility of studying ocean areas until surface wave methods were applied to the problem.

Surface Wave Studies

Surface waves can give information about average crustal and mantle conditions over the entire path traversed. Both Love and Rayleigh waves have been used, and two independent solutions have been obtained. Surface waves are easily observable over paths of continental, oceanic, or even global dimensions. By choosing purely continental and purely oceanic paths, it is possible to make ready comparisons of crustal and mantle structure in the two types of areas.

The effective penetration of surface waves is the order of a wave length. Their velocity of propagation depends upon a sort of weighted average of the elastic properties of the materials down to a depth of the order of a wavelength. By observing surface wave velocity as a function of period, it should be possible to deduce elastic properties as a function of depth. But the calculations are difficult, for in a realistic treatment it is necessary to treat spherical earth models with many layers, including gradient layers. These calculations could not be made until new theoretical methods and large electronic digital computers were available. Further, it was necessary to make some improvements in seismographs to provide suitable data on the longer period surface waves which could "penetrate" several hundred kilometers into the mantle. Specifically, long period vertical seismographs, used with matching horizontals, were required in order to make definite segregation and identification of the longer period Love and Rayleigh waves. Finally, it was necessary to have some assurance that in its topmost part the oceanic mantle had the same properties as the continental mantle. This information, provided by seismic refraction measurements, was necessary as a starting point for the surface wave calculations. Love waves of sufficiently long period, called *G* waves or mantle Love waves, have been studied since about 1926, principally by Gutenberg, Byerly, Imamura, and Satô. Mantle Rayleigh waves were first described in 1954 (Ewing and Press, 1954a, b), and their possibilities as a new and powerful method for investigating upper mantle structure were pointed out.

By 1956 it was becoming apparent that the *G* wave, in its simplest undispersed form, was best observed for purely oceanic paths, for which the fundamental Love mode has nearly constant group velocity in the period range from 20 to 300 sec. The comparison of the *G* velocity, about 4.4 km/sec, with the velocity of 4.7 km/sec for mantle shear waves, obtained from short period surface wave and seismic refraction studies, indicated, even without detailed calculation, the necessity for a low-velocity channel in the oceanic mantle (Press and Ewing, 1956). It was then apparent that detailed calculation of surface wave dispersion in realistic models would help greatly to solve the problems of upper mantle structure.

Satô (1958) used an integral equation to deduce the shear velocity structure from the Love wave phase velocity curve. This structure agreed remarkably well with the velocity distribution of Jeffreys and Bullen(Bullard, 1954, Table 3, p. 83). The calculation was made for a flat earth and, even so, was almost beyond the scope of the desk calculator used.

Landisman and Satô (1958) made calculations of dispersion for Love waves in a flat earth model having two homogeneous layers, overlying a half space with linear gradients in density and shear modulus. They compared their calculations with observations for Love waves from the magnitude 8 Sinkiang shock of 1931, recorded in Japan and Canada, for continental paths, and concluded that "the only shear velocity structures which are concordant with observations of surface wave dispersion and body wave travel times are those containing a low velocity layer in the region from roughly 100 to 200 km below the Earth's surface." This was the first quantitative interpretation of Love wave dispersion which required the existence of the low-velocity zone in the upper mantle. The model used was realistic despite the small number of layers, owing to the gradient in properties of the half space. The data were for continental paths. The continental mantle structure they deduced is shown in Fig. 9 as model 38 km XII.

Press (1959) emphasized the fact that the velocity of *G* waves, 4.41 km/sec, is the same for oceanic and continental paths, and concluded that "the low velocity zone in the mantle is a worldwide phenomenon." This equality of *G* wave velocity led him to suggest "that the composition and distribution of temperature are the same for depths greater than about 50 km under continents and oceans." This conclusion was not based on detailed dispersion calculations and involved debatable assumptions about the relation of *G* waves to continental Love waves.

Landisman *et al.* (1959) presented further cases of the calculations reported by Landisman and Satô (1958). They deduced an oceanic mantle structure by fitting a "typical oceanic Love wave dispersion curve." This was built up from the *G* wave group velocities determined by Satô (1958) for primarily oceanic world-circling paths, plus the oceanic Love wave data of Oliver *et al.* (1955), Coulomb (1952), and Wilson (1940) for periods less than 60 sec. As a result of the calculations for oceanic areas, it was concluded that (1) "the upper mantle beneath the oceans is different from that under continents" and (2) "under oceans, the region of low shear velocities rises to depths of about 50 km." The oceanic mantle structure resulting from this study is shown in Fig. 9 as Oceans VIII. A fuller account of this work will be published in the near future.

Takeuchi *et al.* (1959) applied variational calculus methods to the problem of dispersion of mantle Rayleigh waves. This compared computed phase velocities for the Jeffreys-Bullen and the Gutenberg models of velocity distribution with phase velocity curves obtained by integrating the mantle Rayleigh wave group velocities determined by Ewing and Press (1954a,b). They concluded that the better fit obtained from the Gutenberg model "demonstrates the existence of a low-velocity layer in the upper mantle," and that it must be present under oceans and continents. This work gives no information for comparison of the continental and oceanic mantle, since the original data were specifically limited to a period range in which the ocean-continent contrast produces little effect on Rayleigh wave dispersion.

Dorman *et al.* (1960) compared data on Rayleigh wave dispersion over continental paths and oceanic paths with computations on eleven models of velocity distribution. They concluded that "the

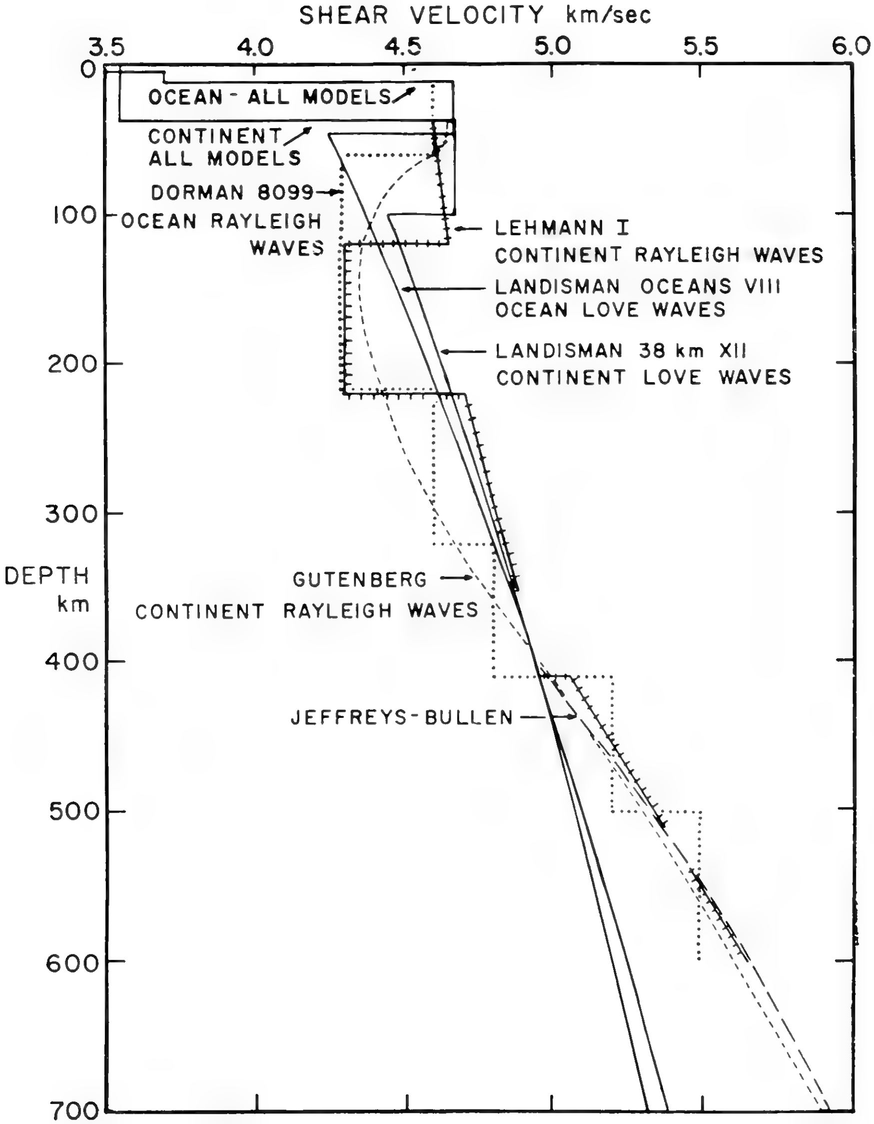


Fig. 9. Shear velocity vs depth, as deduced from studies of shear body waves, Love waves, and Rayleigh waves.

velocity distribution for the continental crust-mantle obtained by Gutenberg and by Lehmann from body wave data, both of which include a region of low velocity in the upper mantle, are consistent with the Rayleigh wave data . . . ".

The detailed investigation of mantle structure from surface wave dispersion data is a young but very active field of study. Rapid progress has been made possible by the introduction of high-speed computing machines. Many details of mantle structure await further study. Outstanding among these is a discrepancy between Love and Rayleigh wave results for shear velocities in the low-velocity zone of the order of 0.1 km/sec. It seems certain that small adjustments in the assumed values of density and Poisson's ratio will lead to a velocity structure which satisfies the data of body waves, Love waves, and Rayleigh waves.

Dorman *et al.* (1960) also studied Rayleigh wave dispersion across oceanic areas and concluded that "It is also clear that the velocity distribution below the depth of the continental M-discontinuity cannot be the same under continents and oceans. Instead, an oceanic model obtained by successive approximation to oceanic Rayleigh wave dispersion data shows that the region of low shear velocity extends to much shallower depths under the oceans, plus being a much more prominent feature under oceans than under continents." These results are in general agreement with the results of Love wave calculations discussed in a previous paragraph, and are shown in Fig. 9 as Dorman 8099 for oceans, and Lehmann I and Gutenberg for continents.

Figure 9 shows a summary of the velocity distributions which have resulted from surface wave studies to date. It shows the principal results and also serves for discussions of the unsolved problems.

The most important unsolved problem is the discrepancy between the structure for continental mantle deduced from Love waves and from Rayleigh waves.

This discrepancy sets in only at a depth of about 100 km, the upper limit of the regions of lower shear velocities. As is well known, all seismic investigations, except those using Gutenberg's inflection point method, whether by means of body waves, Love waves, or

Rayleigh waves, are limited by a lack of uniqueness in the presence of a zone of lower velocities. In addition, all the theoretical models calculated to date have used various approximations to the Jeffreys-Bullen density distribution, shown in Fig. 10, which is based on the Jeffreys-Bullen velocity structure. This velocity distribution, not shown above 400 km in Fig. 9, does not include a low-velocity zone, and for this reason has been found to be incorrect by every surface wave study performed to date, and has since been altered on the basis of body wave data from explosions, supplemented by reinterpretation of earthquake arrivals (Jeffreys, 1958).

New data from various sources require a revision in the density distribution used for the upper mantle. This revision will affect the calculated velocities for Love and Rayleigh waves differently, and is expected to remove the discrepancy. Also, new spherical earth calculations show that sphericity is important, and must be allowed for in these studies.

Finally, a few words are required about the degree to which the various models reproduce the observations of surface wave dispersion. Despite the scatter of Rayleigh wave observations for periods less than 90 sec, it seems certain that new computations

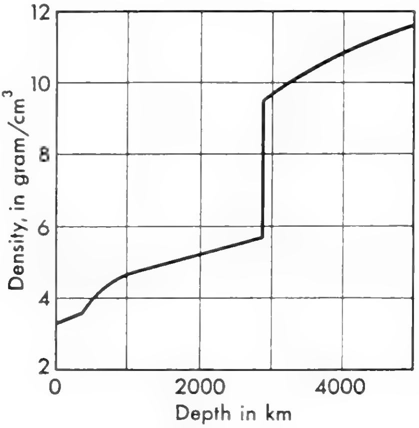


Fig. 10. Density in grams per cubic centimeter vs depth in kilometers for the mantle (after Bullen, from Heiskanen and Vening Meinesz, 1958).

will be required in order to lower the calculated group velocity maximum. [Compare calculations of Dorman *et al.* (1960) with observations of Press and Ewing (1956)]. This alteration can be produced by changes in shear velocity, in density, or in both. With the same density distribution, the derived Rayleigh wave shear velocities are consistently lower than those found for Love waves, when no allowance is made for sphericity.

Comparison of Rayleigh wave continental and oceanic solutions shows a large velocity decrease for the oceans, between 60 and 120 km. Similarly, the Love waves require a sharp drop in shear velocities under oceans between 50 and 100 km.

This surface wave evidence is the most direct and representative evidence obtained to date about differences between the normal mantle structure of continents and oceans. It is now established that (1) the mantle beneath the oceans is significantly different from that beneath the continents and that (2) the low-velocity channel is found at depths of about 50 km, as compared to about 100 km beneath continents.

Other Studies

A summary of present knowledge of the properties of the mantle, based primarily on seismic studies of body waves and surface waves, and concordant with measurements and calculations of thermal, electrical, and other geophysical and geochemical properties gives a broad picture of two main zones or shells which are found beneath nearly the whole of the earth. These are clearly indicated in the velocity-depth curves in Fig. 7.

Beginning at the core-mantle boundary, the lower of these two regions, from about 900–2700 km depth, coincident with Bullen's region D (1953) has been shown by Birch (1952) to be remarkably uniform in elastic properties and, inferentially, in composition. Figure 11 shows Birch's reduced densities to be constant in this region.

It has also been inferred to be quite uniform in temperature by all recent studies of mantle temperature as shown in Fig. 12. McDonald (1957), Fig. 13, has also concluded that the electrical conductivity is nearly uniform in this region.

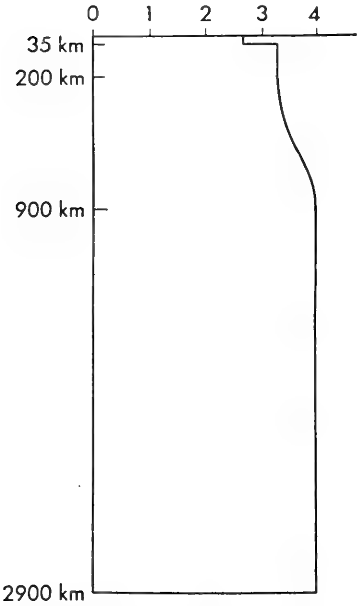


Fig. 11. Density in the mantle in grams per cubic centimeter, reduced to surface temperature and pressure (after Birch, from Heiskanen and Vening Meinesz, 1958).

It is also to be noted that no deep focus earthquakes have ever been found at these depths, indicating that a rate of strain accumulation sufficient to produce earthquakes occurs only above 800–900 km.

Between depths of 900 km and 200 km, all the recent seismic, thermal, geochemical, and electrical studies have been interpreted to indicate a broad zone of transition between the homogeneous lower mantle, and the low-velocity region of the upper mantle, as indicated by the change in reduced densities in Fig. 11. Ringwood (1958) has shown that this transition zone is quite likely to be a region in which iron and magnesium silicates change from their high-pressure spinel lattice structure to the low-pressure olivine crystal lattice structure found at shallower depths.

Benioff (see Fig. 8) has shown that the rate of strain accumulation is remarkably constant in this region between depths of 300 and 800 km.

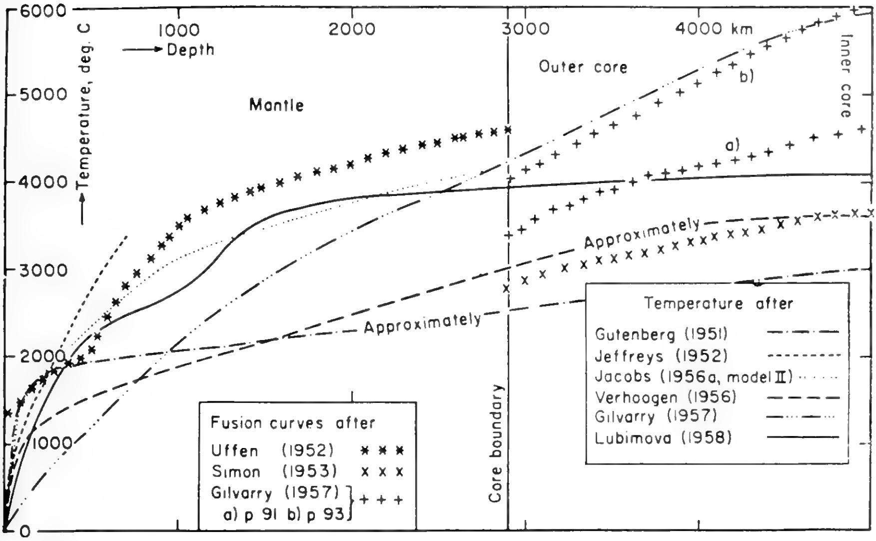


Fig. 12. Calculated fusion temperatures and estimated temperatures in the earth. Some curves are based on graphs preferred by the respective author; others are averages of several graphs or tables. All contain uncertain assumptions (Gutenberg, 1959).

The low-velocity zone, shown in Figs. 7 and 9, extends from about 50 km for oceans and from 100 km for continents down to about 200 km. Lubimova (1958) has calculated lower thermal conductivities in this region (see Fig. 14), and it is quite likely that temperatures approaching the melting point, and consequently much smaller values of shear modulus, must be found in this region. These lower values of shear modulus will of course affect the shear waves more than the compressional waves (Lehmann, 1954).

In Fig. 7 a straight line has been indicated in both the P and S curves. The intercepts of these lines indicate extrapolated surface velocities of about 7.3 and 4.2 km/sec. These are suggestive of the seismic velocities found for the upper mantle in anomalous areas such as the Mid-Atlantic Ridge, parts of the Caribbean area, and some continental margins.

New melting point curves, based on seismic velocity distributions (Uffen, 1952; Gutenberg, 1959), including a region of lower

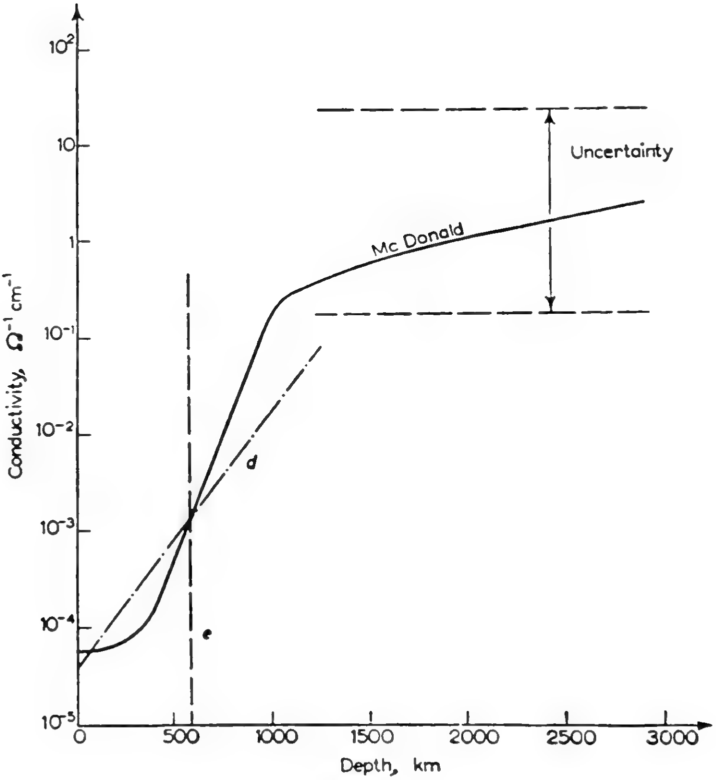
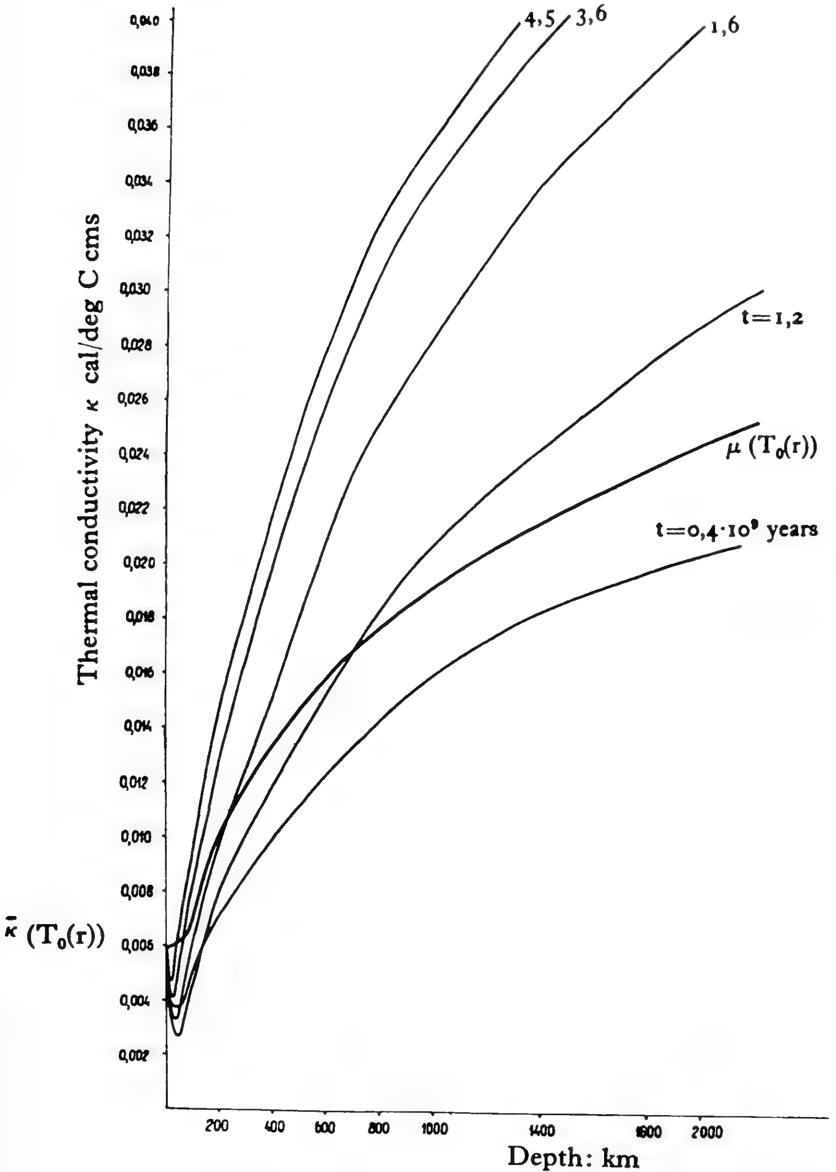


Fig. 13. Electrical conductivity distribution of McDonald for the mantle, with Lahiri and Price's *d* and *e* distributions for comparison (Tozer, 1959).

velocities, will probably show an even closer approach of the melting point curve to the temperature distribution in this part of the mantle. The closer approach of the low-velocity zone to the surface of the earth beneath the oceans might explain the well-known paradox that the nonradioactive oceanic crust shows, despite some variability, average values of heat flow similar to those found for the radioactive crust in continental areas (Bullard *et al.*, 1956; Maxwell and von Herzen, 1959; von Herzen, 1959). Above the low-velocity zone lies the high-speed subcrustal region, which is quite likely to be the lower limit of the lithosphere beneath continental and oceanic regions.



$$\kappa\,(rt) = B\rho^{2/3}\,\frac{u^3\,u^{1/2}}{T^{5/4}} + \frac{16}{3}\,\frac{n^2\,\sigma T^3}{\epsilon} \qquad \epsilon = 40\ \text{cm}^{-1} \quad n = 3$$

Fig. 14. Distribution of thermal conductivity in the mantle (Lubimova, 1958).

The general agreement in depth of the transition from inner mantle to outer mantle (see modified Gutenberg velocity-depth curve, Fig. 7) with the maximum depth of focus of earthquakes suggests that the outer mantle may be a structural as well as a compositional unit.

Further work, both experimental and theoretical, is required to resolve the discrepancy in velocity distributions deduced from body waves, Rayleigh waves, and Love waves, and to use these new velocities to calculate better distributions of density, temperature, melting point, and other physical properties of the mantle.

The contrast between continental and oceanic structure in regard to seismic wave velocities are definitely established to depths of about 100 km. A similar contrast for geothermal properties is being established. The other physical properties of the upper mantle are not yet known in sufficient detail to permit their use in comparison of continental and oceanic areas. Our present limited knowledge about the upepr mantle, however, can lead to decisive judgments of some theories of the origin of continents and ocean basins.

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Forces and Processes at Work in Ocean Basins

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KNOWLEDGE of the ocean floor has grown in a curious way. In 1872 Murray and his colleagues set out in the *Challenger* on a voyage crossing all the oceans. In the course of this voyage they collected samples of the bottom materials, examined them with such care and wrote so solid a report on them that it remained the main source of knowledge of the ocean floor until the 1930's. In retrospect it is odd how little was done during the sixty years after the *Challenger* Expedition. The physicists were otherwise engaged, and the oceans were left largely to the biologists.

In the 1930's there were the first glimmerings of what was to come. By great good fortune Richard Field became interested in the matter and applied his enthusiasm and his unequaled and rather overwhelming powers of persuasion to interest others. Many of those who have contributed to recent developments owe the first impulse directly or indirectly to him. Of course the subject was due for a revival, and there were many other independent new starts: Vening Meinesz's gravity, Revelle's work on the *Carnegie* samples, Piggot's cores, the U. S. Coast and Geodetic Survey's charts of the canyons off the eastern shores of the United States. In all these ways the subject was awakening again when World War II came, and when it was over the great flood of new knowledge about the ocean floor started to accumulate.

Some of the things found were expected, or not surprising, such as the shallow oceanic Moho and the thick sediments beneath the continental shelf, but many, perhaps most, were quite unexpected. No one would have predicted turbidity currents, or flat-topped seamounts, or the high oceanic heat flow. Obviously many more surprises are to come, but things have reached a stage when a tentative review of the processes behind the facts may be useful. The purpose of such a review is not primarily to arrive at a correct account of what takes place. Many of the observations are susceptible of more than one explanation, and there is no great virtue in guessing which is correct and plumping for it. The important thing seems to be to define the range of possible processes and to suggest further observations and experiments that may distinguish between them.

I am suspicious of wide generalizations. To write down the equations of motion and of the theory of the solid state and solve them will tell little about what has happened on the ocean floor. The line of progress seems to be to examine the individual happenings and processes in the light of the principles of physics and chemistry and to hope that the pieces will fit into a wider synthesis. We must avoid forcing dubious or ill-digested details into some preconceived grand theoretical scheme of geological development. The major problems of geology have been with us for a long time and we are not likely to solve them this year or next; but we can use the new knowledge about the ocean floor to see what is the real nature of the problems and we may hope gradually to approach a correct account of present and past processes.

Sedimentation

The 1950's have seen the overthrow of most of the views held on sedimentation in the abyssal plains. There is now no doubt that a large part of the material in these plains is derived from sediment originally accumulated in shallow water, and it is difficult to suggest an alternative to Kuenen's "turbidity currents" as a method of transport. The theory of these currents is in a very poor state. The Reynolds number of a current 10 km long traveling at 10 m/sec is 10^{11}, which is much above that experienced in the largest wind tunnels. The extreme turbulence resulting from such a Reynolds number will assist in keeping material in suspension, but will dissipate energy and makes the long distances traveled over a flat bottom even more surprising. There is no detailed picture of how a turbidity current behaves. From the distribution of sediment it appears to be only a few tens of meters thick and a few 100 m wide. What is its state of motion, how are the turbulent eddies arranged, and what is their size? We have not the least idea, but model and full-scale experiments are not impossible. The experiments that have been made seem insufficiently detailed and not to give the quantities in terms of which the hydrodynamicist usually thinks.

The sediments on rises far from land and out of reach of turbidity currents raise many problems. Their mode of accumulation is clear enough—the material settles from the overlying water—but what is the rate of sedimentation and what period of time is represented by the rather small thickness found? A hole bored through the whole thickness would be of the greatest interest. One could hope that both the potassium-argon and paleontological methods would give ages and rates of sedimentation. Such bore holes would give a lower limit for the age of an ocean basin and would greatly restrict the range of possible speculation. In particular it is important to determine whether the Atlantic Ocean contains sediments older than the Cretaceous.

Continental Shelf

The seismic results and off-shore drilling have shown that the continental shelf is underlaid by a great thickness of sediments which extend in many places below the level of the neighboring abyssal plains. Clearly the shelves are areas of subsidence which have been kept filled with sediments. Since the pile of sediments is approximately in isostatic equilibrium, it is likely that the load has affected the extent to which the subsidence has proceeded, though we do not know if it is the prime cause.

The natural supposition is that sediment from the land is carried out over the continental shelf, where currents and tides usually prevent it from coming to rest, and that it is deposited on the slope between the edge of the shelf and the floor of the deep ocean. On this view the shelf would have the structure shown in Fig. 1*a*. In fact, it appears that this is not so. It has long been known that on the eastern seaboard of the United States, Mesozoic

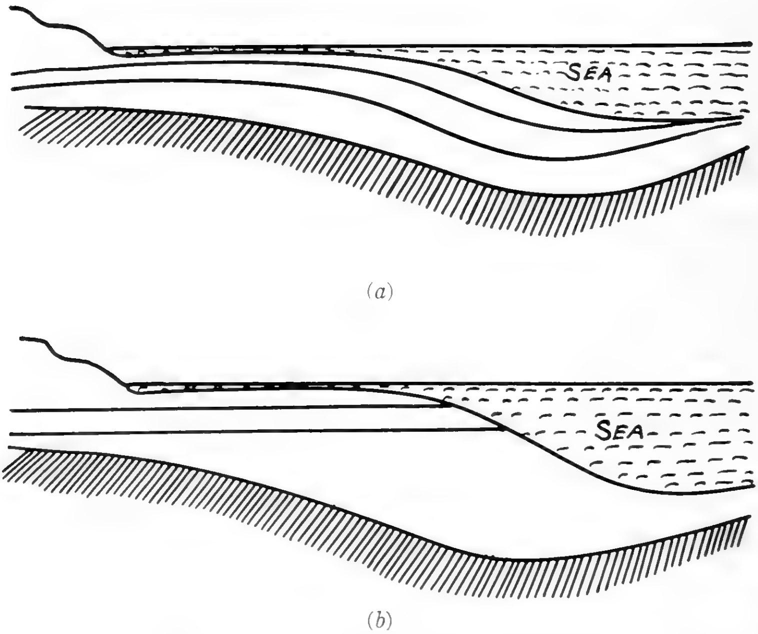

Fig. 1. Sections of the continental shelf.

and Tertiary rocks crop out in the walls of canyons within a short distance of the edge of the shelf, and similar results have been found by M. N. Hill in the mouth of the English Channel. It seems that all the recent sediments are being carried off the slope by submarine landslides and turbidity currents and are coming to rest either in the hummocky area just to seaward of the slope or on the abyssal plains. It may even be that the continental slope is being eroded by the cutting back of canyons. If the structure is indeed as in Fig. 1*b*, and not as in Fig. 1*a*, it is difficult to see how it was formed. Heezen *et al.* (1959) have recently suggested that the continental shelf off the eastern seaboard of the United States started as a trench, comparable to that north of Puerto Rico, and that this became filled. In the course of filling the trench, the shelf is supposed to have formed so that the original landward edge of the trench lies at about the present edge of the shelf. The edge itself would then be a fault scarp caused by vertical movements on the edge of the buried trench.

This suggested history does not seem plausible. Trenches are normally associated with island arcs for whose past presence on the east coast of the United States there is no evidence. It also seems difficult to suppose such very extensive faults to have occurred after the most recent sediments outcropping in the canyons, particularly if the same mechanism is to be extended to other coasts which have similar shelves. The filling of a series of faulted basins, as off the coast of California today or of a gentle downwarp, would seem a more likely early stage of a continental shelf than does an island arc.

All that can be deduced from the observations is that the shelf was formed in at least two stages. In the first, more or less flat lying sediments were laid on a subsiding basement, then a scarp was formed at the outer edge, and the existing regime set in. The scarp could be found by normal faulting, as Heezen *et al.* (1959) suggest, or by erosion or, conceivably, by continental drift splitting a relatively narrow sediment-filled basin and converting it into the shelves of two opposing continents. All such suggestions are guesses with little evidence in their favor and no great chance of being right. However, they do suggest what evidence we should look for. The crucial question is whether the sediments in the basin on the seaward side of the slope contain the missing extension of the shelf, including the foreset beds at its original edge, or whether it is filled with sediments younger than the youngest exposed in the canyons. This can presumably be decided by drilling.

Much information on the structure of the shelf must have been acquired by the extensive reflection shooting by oil companies in the Gulf of Mexico and elsewhere. It is to be hoped that this will some day be made available.

The suggestion that the thick pile of sediments beneath a continental shelf will become in time a geosyncline is a natural one. One could suppose that the blanket of sediments caused a rise of temperature at depth, reduced the yield strength of the rocks, and initiated the crumpling under horizontal compressive stresses. There are certain difficulties in this view. The typical continental shelf does not receive sediment from both sides as many geosynclines are supposed to have done in the past. Perhaps the evidence for the conditions of formation of sediments in geosynclines should be looked at again in the light of our new knowledge of present day marine sediments; we can no longer assume that a coarse, ripple-marked, marine sand was formed in shallow water near shore.

If a shelf is to be converted into a mountain range, a mechanism is required to lower the Moho from about 15 km to 35 km. Two suggestions have been made. If the material below the Moho has roughly the composition of achondritic meteorites, the Moho could be lowered by differentiation of this material into basalt and a more basic rock. If the Moho represents a phase change, the alterations in pressure and temperature due to sedimentation and sinking could drive it to a greater depth. The solution of these problems is of great importance, but it is unlikely to be achieved till we have independent evidence as to the material beneath the Moho.

Submarine Vulcanism

In most places on land, extrusive rocks make a minor contribution to the materials visible at the surface, and volcanos and lava flows are relatively uncommon topographic forms. Terrestrial scenery is predominately the result of folding, tilting, and erosion. In the deep ocean the great majority of topographic features are either piles of lava or fault scarps. The extrusion of lava is therefore one of the key processes in the development of the ocean floor. Unfortunately we know almost nothing about what is going on.

The hard rocks of the ocean are more difficult to collect than are the sediments. Dredging collects material that is lying on the sea floor and it is often difficult to tell whether it has been broken from rock *in situ*, is a locally derived boulder, or is an erratic. The usual opinion is that any unexpected rock, and particularly any piece of granite, gneiss, or schist, is an erratic, though there is often no direct evidence that this is so. A further difficulty is that the rocks are often so decomposed as to be difficult to identify.

The principal requirement is a method of obtaining cores of hard rock long enough to penetrate surface weathering and to give some certainty that a specimen is derived from rock *in situ*, and not from a boulder. Naturally a means of drilling really deep holes would be of the first importance, but a drill that could penetrate only a few feet would also be most welcome.

If good collections of reasonably fresh submarine volcanic rocks can be made, it should be possible to date them by potassium-argon or rubidium-strontium ratios. This would give us the ages of the great systems of ridges and of the groups and chains of seamounts. Nothing would do more to reduce the range of possible speculation.

The great majority of the innumerable seamounts that occur in all the oceans are volcanos, and it seems reasonable to suppose that they were fed from a pipe leading to molten basaltic material either above or below the Moho. The ridges, on the other hand, may be chains of overlapping volcanos or the result of fissure eruptions. The topography strongly suggests faults parallel to the axis of the ridge, and it may be that faults have controlled the outflow of lava.

The first impression that vulcanism is more common at sea than on land may be an illusion since we do not know how long a time span is represented by the volcanos we see. If the oceanic volcanos lasted for much longer periods than volcanos on land, there would naturally be more of them recognizable at a given time. Little is known about the erosion of submarine rocks, and the very decayed state of the large collection made in 1958 by M. N. Hill and D. H. Matthews came as something of a surprise. Matthews has made a study of these rocks and has shown that they have been broken into pieces a few centimeters across and that iron and manganese minerals have been deposited in the cracks. This work has explained the origin of the masses of angular debris frequently seen on photographs and in dredge hauls taken near seamounts. We do not at present know whether this breaking up of the rock takes place immediately on its coming in contact with sea water or whether it is a process that goes on slowly over a long period. If the rock is split and attacked by sea water while still hot, the whole thickness of the rock in a seamount or ridge may be broken up and decayed. The rather low seismic velocities found on the ridges would be consistent with this.

The seismic results suggest that material giving velocities around

4.5 to 5 km/sec occurs not only on the ridges and seamounts but very widely under the areas covered by sediment. It is not certain that the material is the same as in the places where decayed basalt is exposed, but it seems possible and even likely that most of the sea floor is underlaid by such material.

For several kilometers above the Moho, the seismic velocities are usually between 6 and 7 km/sec, and the material is usually supposed to be basalt. We have no evidence whether this is an original part of the ocean basin or whether it has been formed by some long continuing process. It may be a continuous body of solid basalt or it may be a series of flows analogous to the plateau basalts of the continents and perhaps with sediments lying between the flows.

There would be considerable difficulty in accounting for the melting of material above the oceanic Moho. A heat flow of 2×10^{-6} cal/cm^2 sec, which is probably above the average, would give a temperature of under 200°C at the Moho even if all the heat came from greater depths. The best hope of explaining the widespread oceanic vulcanism and the relatively high heat flows seems to be to suppose that both the heat and the lava come from below the Moho. It also seems likely that the radioactivity of the upper part of the mantle must be nearer to that of basalt than to that of dunite. (For a more detailed discussion see Bullard *et al.*, 1956.) Whether the basalt is formed from the material of the mantle by differentiation or by a phase change is unknown.

Clearly many of the uncertainties of the processes occurring in the ocean basins center round the extrusive rocks. The reason for this is largely the difficulty of collecting them. It is to be hoped that the proposed attempts to drill deep holes at sea will succeed and will provide the samples that are so desirable.

The Larger Pattern

The pattern of the ocean floor is dominated by linear features: ridges, chains of islands, fracture zones, and trenches. The major features of continental structure, the fold mountains and their remains represented in the shield areas, appear to be absent from the oceans. It is obviously of importance to determine what happens to a continental or an oceanic structural feature when it meets the continental edge.

In many places, particularly in North America, the fold mountains run parallel to the edge of the continent, but in Europe there are several places where folding runs almost at right angles to the edge. There is no topographic evidence for a continuation of any of these features beyond the continental edge, and the same is true of the Appalachian folding where it meets the sea to the north of Newfoundland. It is possible that there are submarine extensions of these lines of folding which are buried beneath the sediments of the continental slope and abyssal plains. If so it should be possible to discover them by magnetic and gravity surveys. A start has been made by M. N. Hill and T. D. Allan, who are making a magnetic survey off the end of the Brittany peninsular. The results of this and similar investigations are of crucial importance since it is difficult to conceive that a continent could be folded along an axis at right angles to the coast without disturbing the sea floor on the seaward extension of the line of folding. It is of course geometrically possible to imagine that the north-south movement involved in the folding terminates on a north-south transcurrent fault hidden beneath the continental shelf, but the sinuous form of the west coast of Europe does not suggest such a feature.

The structural lines of the North Atlantic are, on the whole, parallel to the continental edge (apart from the rather vague ridge running from the Azores toward the south coast of Spain). In the Pacific, however, there is a series of parallel fracture zones, some running for over a thousand miles across the ocean floor and approaching the west coast of the United States and Mexico (Menard and Fisher, 1958). It is extremely striking that these great features are not a continuation of any comparable features on land. The Mendocino escarpment and the Murray fracture zone may be connected in some way with the San Andreas fault but they are certainly not continuations of it. It has been suggested (Menard and Fisher, 1958) that the Clipperton fracture zone and the associated Tehuantepec ridge are continued across Central America and reappear in the Caribbean, but the connection does not seem at all firmly established. Menard and Fisher have also suggested that fracture zones in the northeast Pacific are continued in China.

There seems to be substantial evidence that in the Atlantic and the Pacific the structures of the continents and the oceans are rarely directly connected. Obviously the evidence is not sufficient to establish such a generalization, and the object in proposing it is largely to suggest things that should be looked for. Particular interest attaches to structures, such as the Cameroons and the Lomonosov ridge, which may represent trends crossing the continental edge.

If the fold lines of western Europe and of Newfoundland are cut off between the shore and the edge of the continental shelf, it would strongly suggest that the ocean floor was not present when the folding took place and would be consistent with the hypothesis of continental drift. New evidence on this has come from paleomagnetism; the whole material has recently been reviewed by Blackett *et al.* (1960), who make a strong case for relative movements of the continents. The evidence seems strong enough to justify the effort needed to obtain some independent check; a continuation of Caledonian or Hercynian structures from Europe well out into the Atlantic would go a long way to show that the ocean had not been formed by a post-Paleozoic westward movement of America.

Paleomagnetic studies cannot detect a movement in longitude; particular interest therefore attaches to any evidence that can be found for east-west movements from a study of the oceans. Many of the arguments that have been suggested are inconclusive. The observed general similarity of crustal structure in the Atlantic and Pacific is perhaps not to be expected if the Atlantic is a recently opened gap. The mid-Atlantic ridge and particularly its central valley might be regarded as the place where the Atlantic is at present widening. The continuation of this feature round the south of Africa and up the Indian Ocean to the Red Sea suggested by Rothé (1954) and by Ewing and Heezen (1956) is consistent with the movement of India away from Africa and with an incipient splitting of Africa from Arabia (Girdler, 1958). Such an explanation is not, however, available for the ridges of the Pacific which are supposed to be connected with the ridges of the Indian Ocean and thus with the mid-Atlantic ridge. It is important to be sure of the various suggested connections and to know how far the ridges are really similar. In particular, do the Pacific ridges often or usually lack a central valley as has been suggested by Menard (1958)?

It has been suggested (Hope, 1959, summarizing Russian work) that the Lomonosov ridge which crosses the Arctic Ocean is a folded feature connecting the Verkhoyansk range of Siberia to Ellesmere Island. Obviously the ends of this ridge could only remain attached to Asia and to Ellesmere Island while North America moved through 70° in longitude if it were considerably distorted. It therefore seems of great interest to examine the materials and date of this ridge and the form of the connections with the continents at both ends.

If the continents are moving, there must be horizontal forces, and the only plausible suggestion that has been made is that these forces are associated with convection currents in the mantle. The high heat flows found on the mid-Atlantic ridge and on the east Pacific rise suggest that, if the currents exist, their rising limbs are under the midocean ridges. The rising current would be of lower density than the material on each side and would explain the rough isostatic compensation of the ridge. Hess (1954) has also provided an alternative explanation depending on serpentization of material beneath the ridge which does not appear inconsistent with a rising current beneath it.

Obviously, views about the existence of convection currents and continental drift must be tentative. The mechanisms, if they exist, are concealed so effectively and have such long time scales that they cannot be directly observed. Theory cannot assert or deny the possibility of such processes. If the facts show a high probability that they have occurred, we must make the best theory we can, but we should not place too much reliance on it or let it obscure the very complicated facts.

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Stratigraphy of the Deep-Sea Floor*

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STRATIGRAPHY is that branch of geology which deals with the formation, composition, sequence, and correlation of the stratified rocks of the earth's crust. Studies are mainly concerned with the sedimentary rocks, but they also deal with other layered rocks such as ash beds, lava flows, and metamorphosed sediments.

Stratigraphy can be divided into three phases (Dunbar and Rodgers, 1957): (1) the description of the strata as they occur in sequence in local areas; (2) the correlation of these local sections: the determination of their mutual time relations and their place in the standard scale that forms the framework of geologic history; (3) the broad philosophy, of great interest to all earth scientists. The first two are important in practical studies and occupy much of the time of geologists employed by oil and mining companies. Stratigraphy provides the raw material which forms the basis for understanding the historical geology of the earth, the changing patterns of continents and ocean basins, the fluctuations of climates, and, through stratigraphic paleontology, the history of the evolution of life on earth. Stratigraphy is primarily a science of integration (Krumbein and Sloss, 1951). The integration of data from diverse fields is possible only when the person attempting it is familiar with the results in these diverse fields.

For the past hundred and more years, the stratigraphy of land deposits has occupied the interests of geologists, and the broad outlines of continental stratigraphy are well established, save for the pre-Paleozoic. For the greatest portion of the globe, namely

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* This paper is a shorter version of two other papers. The first paper, "Thickness and consolidation of deep-sea sediments" has been published in the *Bull. Geol. Soc. Am., 70* (1959); the second paper, "Ocean basin ages and amounts of original sediments," will be published in the *J. Sediment. Petrol., 30,* 370-379 (1960).

the deep-sea floor, the work is barely begun. Only in the past three decades have large-scale efforts on a continuing basis furnished the descriptive material for stratigraphic interpretations. The first valid rough draft of the geologic history of the world awaits the conclusions of the marine geologists and other oceanographers. The sediments and rocks of the deep-sea floor will, in the end, yield the raw material for the unraveling of the earth's history. Of prime importance will be the thickness of sediments and rocks in the deep-sea floor, their total volume, their ages, and geochemistry. The geochemical balance of the world cannot be ascertained until the true thickness, amounts, and kinds of mineral solids in the sea floor are determined; this information will also bear on, if not solve, the problem of the ages of ocean basins.

Here will be mentioned some of the presently available data concerning the gross stratigraphy of the deep-sea floor, namely the large-scale layering in the ocean floor. After two decades of seismic research at sea (by far the greater part concentrated in the late 1940's and the 1950's) it has been shown that in many areas a topmost layer of unlithified sediments overlies layers of higher seismic velocity. The material of the layers immediately under the unlithified sediment has been thought to be granite, lava, pyroclastics, metamorphics, sedimentary rocks, and mixtures of these rocks and others of appropriate velocity.

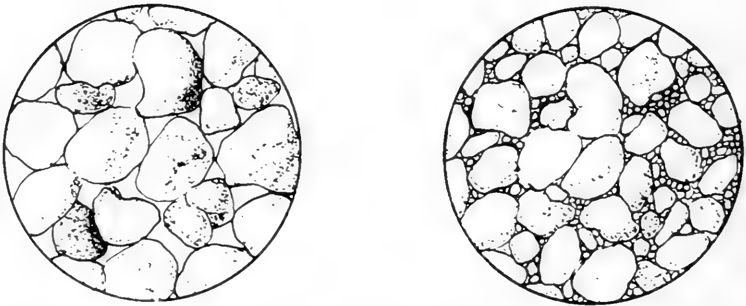
In 1956–1959 evidence increased to indicate that the higher velocity layers can be sedimentary rocks. In 1957, Laughton, and also Nafe and Drake pointed out that the known velocity gradient in the upper sediments is too great to be explained by compaction alone and must reflect the existence of cementation and recrystallization. Hamilton (1957) enumerated physical factors which make it probable that these higher velocity layers are sedimentary rock. Hill (1957) and Gaskell *et al.* (1958) stated that around volcanic islands the second layers may be volcanic, but in the deep-ocean basins it is much more plausible to ascribe them to a sedimentary origin. Ewing and Ewing (1959) suggested that part of the geologic column computed to have a sedimentary velocity may be high-velocity rocks masked by the geometry of the water-sediment column. Their sections are labeled "unconsolidated," "semiconsolidated," and "consolidated" sediment, with the term "consolidated" indicating lithification.

The consolidation and lithification of deep-sea sediments, the velocities of compressional elastic waves to be expected as a consequence of such changes, and the probability that the second layers, in many areas, are lithified deep-sea sediments will be discussed here.

Consolidation of Sediments

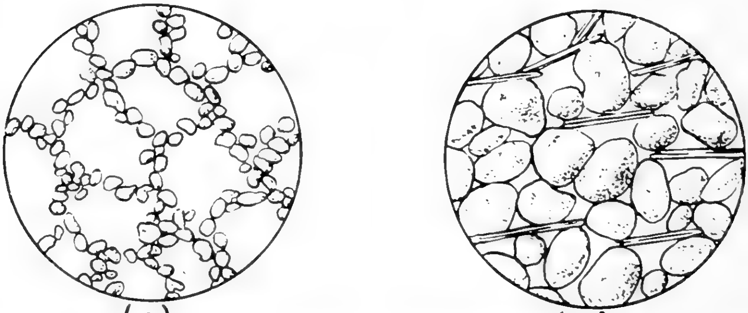
When a sand or coarse silt is deposited, it rolls into a position supported by other grains; intermolecular forces are too small to be effective. When a fine silt or clay is deposited, it is likely to adhere to the grain with which it first comes in contact, owing to intermolecular attractive forces. For a long time the structure of a clay deposit was thought to be that in Fig. 1*e*. Recent work by Rosenqvist (1959) and others using the electronic microscope has shown that the structure of a marine clay is more like the "house of cards" structure in Fig. 1*f*. Each mineral grain of the clay-size particles has its own adsorbed water layers which merge gradually into the free water within the pore spaces. We know from analysis of deep-sea clay, for example, that this pore space, filled with water, may comprise more than 80% of the sediment.

When a natural or man-made load is applied to this last structure, the volume decreases because of the escape of water from the pores. The rate of volume reduction or consolidation is primarily dependent on the amount and rate of load application and the permeability of the sediment. In a sediment with an impervious base, the escape of the water is through the water-sediment interface. When a load is suddenly applied to a sediment structure as, for example, during the construction of a building, the load is at first borne by the porewater as excess hydrostatic pressure, but it is gradually transferred to the sediment structure as the sediment slowly consolidates under the new load. Primary consolidation is completed when the excess porewater pressure is zero. A secondary consolidation may continue for some time; it is thought to be due to the plastic deformation of grains and of the adsorbed



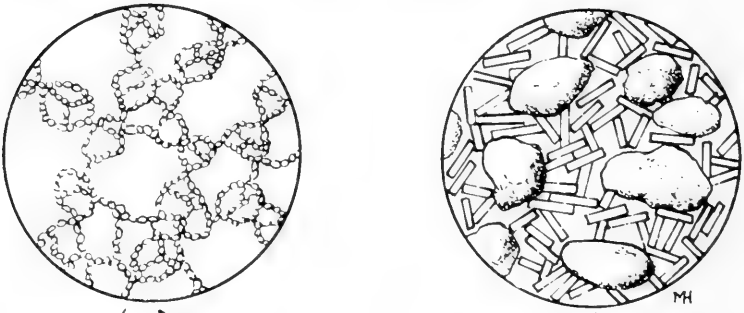
(a) SINGLE-GRAINED STRUCTURE

(b) MIXED-GRAINED STRUCTURE



(c) HONEYCOMB STRUCTURE

(d) BRIDGING EFFECT OF PLATY MINERALS



(e) HONEYCOMB-FLOCCULENT STRUCTURE

(f) CARDHOUSE STRUCTURE MARINE CLAY

Fig. 1. The structure of common sediments.

water around the grains (Taylor, 1948, and others). When the rate of load application is very slow, Taylor (1948) and Laughton (1957) thought it possible that minute loads would cause almost no excess porewater pressure and consolidation,* therefore, will be almost entirely secondary. It would appear that the extremely slow deposition on the deep-sea floor, resulting in minute load applications, would cause no excess porewater pressure.

Consolidation Testing

The consolidation behavior of a clay is studied by running a consolidation test in the laboratory on relatively undisturbed samples and on remolded samples of the same sediment. The sediment is placed in a ring with porous discs at top and bottom. A load is applied to the top disc, and the water is permitted to flow through the discs until deformation of the sediment has practically ceased. The amount of deformation is measured on a dial gage. When the rate of deformation becomes very small, a new load increment is added. The results of such a test are plotted as the void ratio, e, (volume of voids divided by the volume of solids) versus the corresponding total pressure, p. When plotted on semilogarithmic paper the curve is called, in soil mechanics, an e-log p curve and is used in the analysis of settlement which might be expected under given design loads.

After overburden and other load pressures are computed for an actual condition, one can enter the e-log p plot along the pressure line and pick off the corresponding void ratio for the particular pressure. When examining a number of e-log p plots for clay one is struck by a very significant and important fact: no matter how porous the original material, by the time that it is under about 100 kg/cm^2 of pressure the void ratio has usually decreased to

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* The term "consolidation" is used in soil mechanics to refer to a process and not to the solidity of material, which is the geologic usage. It is possible for a material to be completely consolidated (under a certain load, or overburden) and still be relatively soft. "Lithified sediment" is probably a better term to indicate that a sediment has been cemented into a rock. In engineering parlance "compaction" is reserved for artificial reduction of pore space, as with a sheep's-foot roller.

about 0.3 to 0.5 (porosity approximately 29%). Figure 2 illustrates this fact and shows the funneling effect derived when a number of plots are made for different clays; this convergence is even more marked at pressures greater than about 100 kg/cm². This phenomenon allows the use of generalizations in studying the effects of overburden pressures on consolidation even though the exact sediment type (in the silt-clay range) and void ratios at the site are largely unknown. The curves from Skempton (1953) (Fig. 2)

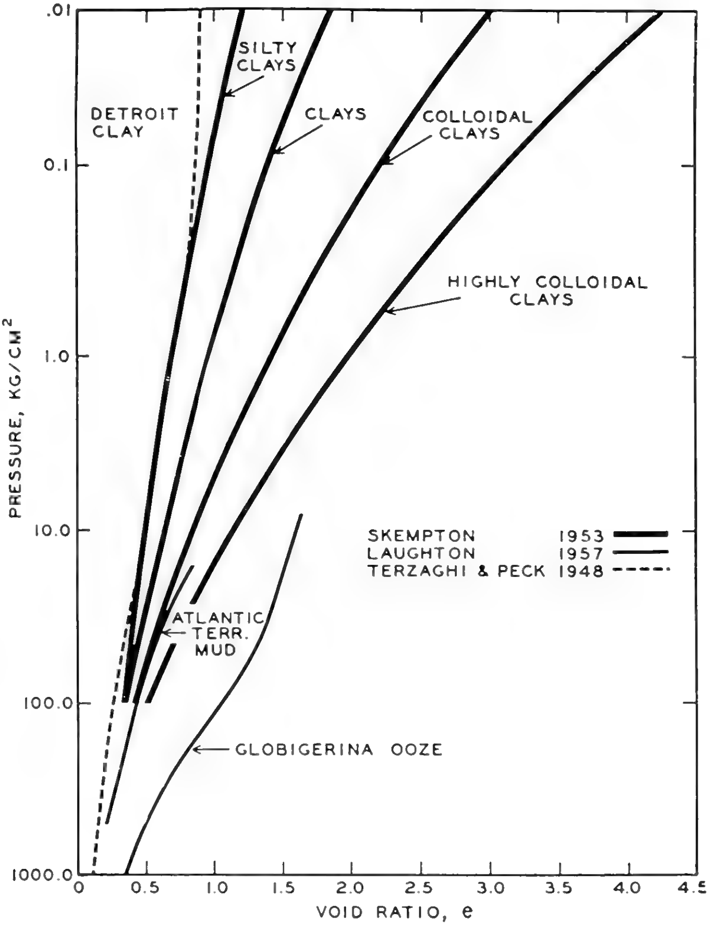

Fig. 2. Consolidation (e - log p) curves for clay and *Globigerina* ooze.

are derived from a large number of field and laboratory determinations which are in accord with a large number of plots from other sources collected by the writer, but not shown on the figure to preserve clarity. Laughton (1957) has published results of consolidation-velocity studies on deep-sea materials. Laughton's *e*-log *p* curves (Fig. 2) have been added to the curves of Skempton (1953) and of Terzaghi and Peck (1948).

Discussion

The difference in the consolidation behavior of sand and clay has long been known and studied in soil mechanics. Sands, after a quick mechanical rearrangement of particles, will show relatively slow decreases of porosity under increasing pressure. The adsorbed water layer, if any, around sand grains is unimportant in this consolidation history. Clay, on the other hand, shows a relatively fast decrease in porosity with increasing pressure and with expulsion of both the porewater and the adsorbed water around the grains. Figure 3 illustrates these differences at pressures greater than 50 kg/cm^2. Mixtures of sand and clay will have

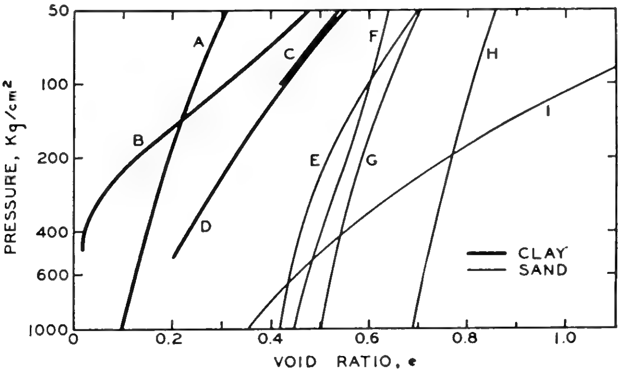

Fig. 3. Consolidation (*e* - log *p*) curves for clay and sand. A, soft Detroit clay; B, shale with hydrostatic uplift (porosity data from Skeels, 1950); C, colloidal clay (Skempton, 1953); D, terrigenous mud (Laughton, 1957); E, 80% sand and 20% mica; F, dense sand; G, 90% sand and 10% mica; H, loose sand (A and E–H from Terzaghi and Peck, 1948); I, *Globigerina* ooze (Laughton, 1957).

consolidation curves intermediate between clay and sand, but always on the high porosity side of clay at the same pressure (Fig. 3).

The difference between the porosity of a calcareous ooze and a clay at the same pressure and depth is quite distinctive: the clay porosity is always less than that of the ooze. *Globigerina* ooze is largely composed of shells, or tests, of planktonic Foraminifera; mechanical analyses of typical calcareous oozes (Revelle, 1944, pp. 144–147) show that the size distribution of particles is such that most calcareous oozes can be considered as very specialized types of sandy silt or sand-silt-clay. It should not be surprising, therefore, if the behavior of *Globigerina* ooze, or calcareous ooze, under gravitational pressure follows the consolidation curves expected for sandy silt or silty sands. In addition, calcareous ooze is a specialized sandy silt in that many of the grains are hollow shells of calcium carbonate; these delicate shells after crowding together under compaction will crush much more easily than typical shallow water sandy silt grains. It should be expected, then, that calcareous ooze will show a faster decrease in porosity than typical quartz particle sediments. Figure 3 illustrates this for the ooze which Laughton compacted. This should also be true of other similar oozes of high calcareous shell content.

How close do the laboratory determinations come to the actual consolidation in the field; both as to settlement under buildings or under gravitational consolidation due to the weight of the sediment itself? This matter has been extensively studied, and it is known that the laboratory results allow close prediction of the actual consolidations (Skempton, 1953; Schmertmann, 1955). Usually the laboratory-derived void ratios are slightly less than those in the field at a given pressure; this is thought to be due to loss of strength because of disturbance during sampling.

The intergranular pressure (owing to the weight of sediment grains) which is used in computations of consolidation is independent of the depth of the water as long as free movement of the water can take place, so that the excess porewater pressure can become zero. The question of hydrostatic uplift (or buoyancy of mineral particles due to Archimedes' principle) is important in computing pressures within the sediment. Several lines of evidence indicate the probability that hydrostatic uplift is near 100% in the upper sediment-rock column to the depts considered in this study. In 1936, Terzaghi found hydrostatic uplift was effective up to 99% in a stiff, plastic Tertiary clay of low permeability, and, in concrete, with porosities as low as 13%, it was 100% effective. In the field of soil mechanics, 100% hydrostatic uplift is allowed regardless of the thickness of clay strata. In oil field reservoirs, pressures are usually hydrostatic and not the combined pressure induced by the weight of the rock and the water. In some sealed reservoirs, however, the pressure is that of the rock and the water (Levorsen, 1954).

The porosity-depth curve (Fig. 4) for Tertiary sediments and shale of the Gulf Coast (Dickinson, 1953) is close to the computed curves for clay with 100% hydrostatic uplift. These Gulf Coast sediments and rocks were deposited in continuous sequence without major unconformities and usually have the normal or hydrostatic pressure* at depth. The position of the curve, and the reservoir pressures, argue for full hydrostatic uplift of the mineral grains of the rock. It should be expected that curves for shale will lie on the low porosity side of those for clay: cementation should effect a reduction of porosity not present in clays.

In generalizing the consolidation characteristics of clay I used one of Skempton's (1953) median curves for clay and the porosity-pressure relations of thick shale sections as derived by Skeels (1950) for a large number of shale sections. For calcarous ooze Laughton (1957) data were used. After the overburden pressures are computed,. the curves can be entered and the void ratio expectable under that pressure can be determined. Knowing the properties, or assuming reasonable properties, for the sediment at the water-sediment interface, it is then possible to construct a table showing the probable variations of various properties at depth in the sediment using standard soil mechanics computations (Tables I and II). From the tables, curves can be drawn

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* For the purposes of this paper all pressures are computed for full hydrostatic uplift.

TABLE I. Consolidation of Clay and Shale (curves from Skeels, 1950; Skempton, 1953)[a]

Depth in Sediment, m	Interval Pressure, kg/cm²	Cumul. Pressure, kg/cm²	Void Ratio, *e*	Density Sat., gr/cc	Submerged Wt., gr/cc	Porosity, *n*, %
0	0	0	2.58	1.40	0.35	72
10	0.35	0.35	1.73	1.52	0.47	63
20	0.48	0.83	1.48	1.55	0.50	60
30	0.51	1.34	1.35	1.58	0.53	58
40	0.54	1.88	1.25	1.60	0.55	56
50	0.56	2.44	1.18	1.63	0.58	54
60	0.59	3.03	1.13	1.64	0.59	53
70	0.60	3.63	1.08	1.66	0.61	52
80	0.62	4.25	1.05	1.67	0.62	51
90	0.63	4.88	1.02	1.68	0.63	50
100	0.63	5.51	0.98	1.69	0.64	49
150	3.3	8.8	0.87	1.72	0.67	47
200	3.5	12.3	0.80	1.76	0.71	44
250	3.6	15.9	0.75	1.77	0.72	43
300	3.7	19.6	0.70	1.80	0.75	41
400	7.7	27.2	0.58	1.85	0.80	37
500	8.1	35.3	0.54	1.87	0.82	35
600	8.3	43.6	0.50	1.90	0.85	33
700	8.6	52.2	0.47	1.91	0.86	32
800	8.7	60.9	0.43	1.93	0.88	30
900	8.9	69.8	0.40	1.95	0.90	29
1000	9.1	78.9	0.37	1.97	0.92	27
1500	48.4	127.3	0.25	2.06	1.01	20
2000	52.8	180.1	0.15	2.15	1.10	13

[a] Assumption: 300 m of clay overlie shale with 100% hydrostatic uplift effective. Properties: density of solids, 2.31 gr/cc; water density, 1.05 gr/cc; initial porosity, 72%.

which illustrate the variations of the various properties with depth. In Figure 4 there are several noteworthy points: (1) a fast decrease in porosity to 38 to 45% at depths between 150 and 300 m; (2) little difference between the curves computed for clay with a grain density of 2.70 gr/cc and that for a clay with 2.31 gr/cc based on the average of 18 determinations on Pacific red clay; (3) the very close likeness of the computed curves to the actual conditions in the Tertiary of the Gulf Coast area; (4) the marked difference between the porosities of clay at depth and that for a calcareous ooze.

Table II. Consolidation of a *Globigerina* Ooze[a] (curve from Laughton,[b] 1957)

Depth in Sediment, m	Interval Pressure, kg/cm^2	Cumul. Pressure, kg/cm^2	Void Ratio, e	Density Sat., gr/cc	Sub-merged Wt., gr/cc	Porosity, n, %
0	0	0	1.90	1.62	0.57	66
10	0.57	0.57	1.88	1.62	0.57	65
20	0.57	1.14	1.85	1.63	0.58	65
30	0.58	1.72	1.82	1.63	0.58	65
40	0.58	2.30	1.80	1.64	0.59	64
50	0.59	2.89	1.78	1.64	0.59	64
100	3.00	5.89	1.68	1.66	0.61	63
200	6.2	12.1	1.56	1.69	0.64	61
300	6.5	18.6	1.49	1.71	0.66	60
400	6.7	25.3	1.44	1.72	0.67	59
500	6.8	32.1	1.40	1.73	0.68	58
600	6.9	39.0	1.36	1.74	0.69	58
700	7.0	46.0	1.32	1.76	0.71	57
800	7.2	53.2	1.27	1.77	0.72	56
900	7.3	60.5	1.23	1.79	0.74	55
1000	7.4	67.9	1.18	1.80	0.75	54
1500	39.0	106.9	1.01	1.87	0.82	50
2000	42.5	149.4	0.88	1.92	0.87	47

[a] Assumptions: A progressive porosity decrease under pressure with *no* lithification which is probably a rare situation. Properties: density of solids, 2.69 gr/cc; water density 1.05 gr/cc; initial porosity, 66%.

[b] Laughton ran the test on a *Globigerina* ooze with 54% $CaCO_3$.

Lithification of Clay and Calcareous Oozes

Clay

The process by which a silt or clay is consolidated and lithified to form a shale was studied by a number of persons in the decade 1925 to 1935. In his classic study Hedberg (1936) used a combination of soil mechanics knowledge and a field study of undistorted shales in Venezuela to investigate the relationship of pressure, depth, porosity, density, and lithification. Hedberg mentioned at the start of his study that there could never be an exact quantitative solution to the relations between pressure, volume, and lithification in clays and shales because there were too many variables,

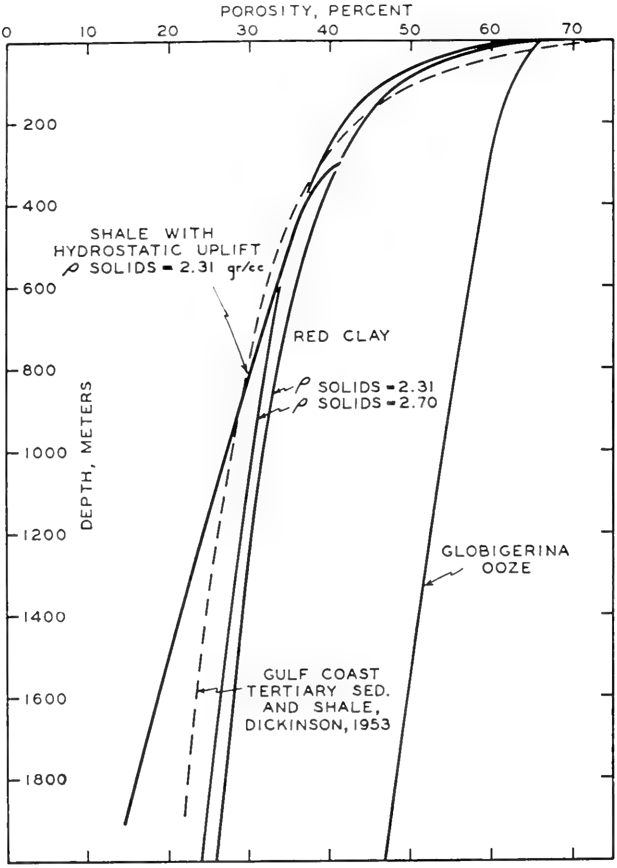


Fig. 4. Porosity vs. depth below the sea floor for red clay and *Globigerina* ooze with hydrostatic uplift. A curve is shown for Skeels' shale (1950) assuming 300 m of unlithified clay overburden and hydrostatic uplift of solids; actual field conditions are shown for the Tertiary of the Gulf Coast (Dickinson, 1953).

but that generalizations were possible for the argillaceous sediments.

During the mechanical rearrangement stage (90% to 75% porosity), under gravitational pressure, free water in pore spaces is squeezed out together with some adsorbed water. During the dewatering stage (75% to 35% porosity) the expulsion of free water continues; adsorbed water moves from points of maximum stress into the larger pores (Fig. 5). With increasing pressure there is a virtual grain-to-grain contact. At this stage only a small part of the adsorbed water remains and almost all the free water is gone. Then, if the pressure is removed, there is some "elasticity" or rebound due to the reattainment by each particle of its film of adsorbed water. Modern studies (e. g., Lambe, 1953, p. 32) affirm that Hedberg's (1936) concept is essentially correct.

When the porosity is below about 35%, the primary consolidation is virtually complete and further consolidation is the result of plastic deformation and crushing of grains. Chemical readjustments begin and there is pressure-point solution and redeposition in adjacent regions under lower stress; colloidal matter tends to crystallize with the formation of new minerals. At lower porosities, cementation and further chemical readjustments (e. g., recrystallization) result in low-porosity shales. Laughton (1957) has noted a definite lamination of clays under pressure in the laboratory and pointed out that this corresponds to the first stages of the formation of shales and laminated mudstones.

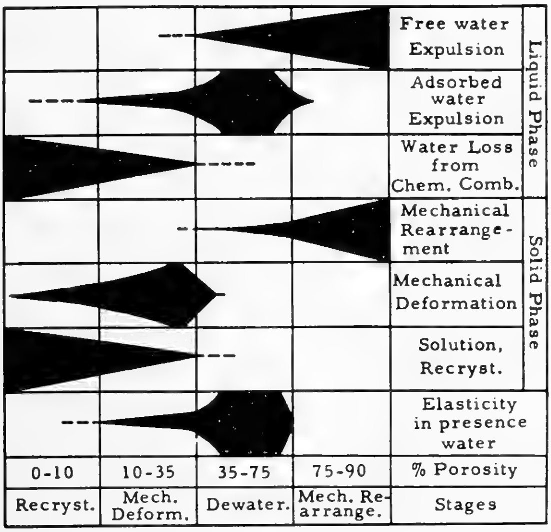


Fig. 5. Processes in the consolidation and lithification of clay (Hedberg, 1936).

An interesting and significant question in the foregoing sequence of consolidation is: at what point does the clay cease to be an "unconsolidated" sediment, become lithified and called "shale"? This transition, according to the foregoing hypothesis, apparently comes at around 35% porosity, when, due to chemical changes, cementation between the grains imparts a rigidity to the structure which previously was not present (Fig. 4). Skeels (1950) noted shales with porosities up to 43%; Birch *et al.* (1942) recorded a highest shale porosity of 45%.

Obviously the change from a clay to a shale will occur at different depths and porosities dependent on pressure and chemical effects, but a reduction to porosities between 35% and 45% is indicated by hypothesis and field data to be the usual range when clay turns to shale. The appearance of the porosity-depth curve previously shown indicates that these porosities should be reached at depths between 150 and 700 m depending on chemical factors and grain densities, and with an average depth, around the area of maximum curvature, of about 200 to 400 m.

Calcareous Ooze

The depth in a sediment column at which lithification of calcareous material begins is not as well indicated as for a clay shale. Calcium carbonate is easily cemented and replaced by other minerals and without great pressure; this is evidenced by the formation of beach limestone and by the occurrence of high-porosity foraminiferal limestones on the tops of seamounts (to be mentioned later). The factors involved in the lithification of calcareous ooze should normally be the same as those for clay shale: pressure, age, and chemical factors being the most important. If calcium carbonate is relatively easy to convert into rock, then one would expect that the depth to lithification in a calcareous section would certainly be no greater (and might be less) than that in a clay-shale section. This would place the expected limits on the thickness of any topmost unlithified section at about the same depths as in a clay-shale section, that is, 150 to 700 m with average depths nearer 300 to 400 m. Areas of faster accumulation might have greater thicknesses of unlithified sediment, as it is known

(Weatherby and Faust, 1935; Faust, 1951) that there is a definite relationship between age and lithification; older sediments have had a longer time to be altered by chemical actions.

After a calcareous ooze has been lithified to limestone, it has a strong, rigid structure. It is unlikely that further deposition causing increasing overburden pressures would cause any marked reduction in porosity. Porosities in limestones should decrease owing to chemical changes, but the marked reduction of porosity because of depth, so well known in shale, will not occur. This is borne out by depth-porosity diagrams in limestone from oil well data (Wyllie *et al.*, 1956; Hicks and Berry, 1956). These factors allow relatively low porosities in rock near the surface having little to do with pressure-induced consolidation. Tables I and II and Figs. 1–5, therefore, are merely suggestive and do *not* illustrate expected porosities at depth for lithified calcareous material. The transition between cemented and uncemented material is likely to be relatively sharp, not gradational.

In the deep sea, including seamounts, but excluding the coral atoll environment with its coralline algae and coral, the known occurrences of *foraminiferal limestone* are rare. Murray and Lee (1909, p. 22) recorded three instances (one each by the *Albatross*, *Challenger*, and *Britannia*) when hardened *Globigerina* ooze was dredged from the sea floor. The Scripps Institution—U. S. Navy Electronics Laboratory Expedition in 1950 dredged indurated calcareous ooze in the form of foraminiferal limestone from four seamounts in the mid-Pacific Mountains west of Hawaii and from one seamount in the northern Marshall Islands. The geology and paleontology of this material is described in detail elsewhere (Hamilton, 1953, 1956; Hamilton and Rex, 1959). Five samples (cf. Fig. 6) examined in great detail (including determinations of the velocity of the compressional elastic waves) are very important in considering the possibility that normal sedimentation can explain part of the present concepts of sea floor structure based on seismic studies. The grain densities (plus other studies) indicate that some of the material has been phosphatized; porosities ranged from 5 to 68% and velocities ranged from 1.77 to 5.46 km/sec at room temperature and pressure (Table III). In short, we would

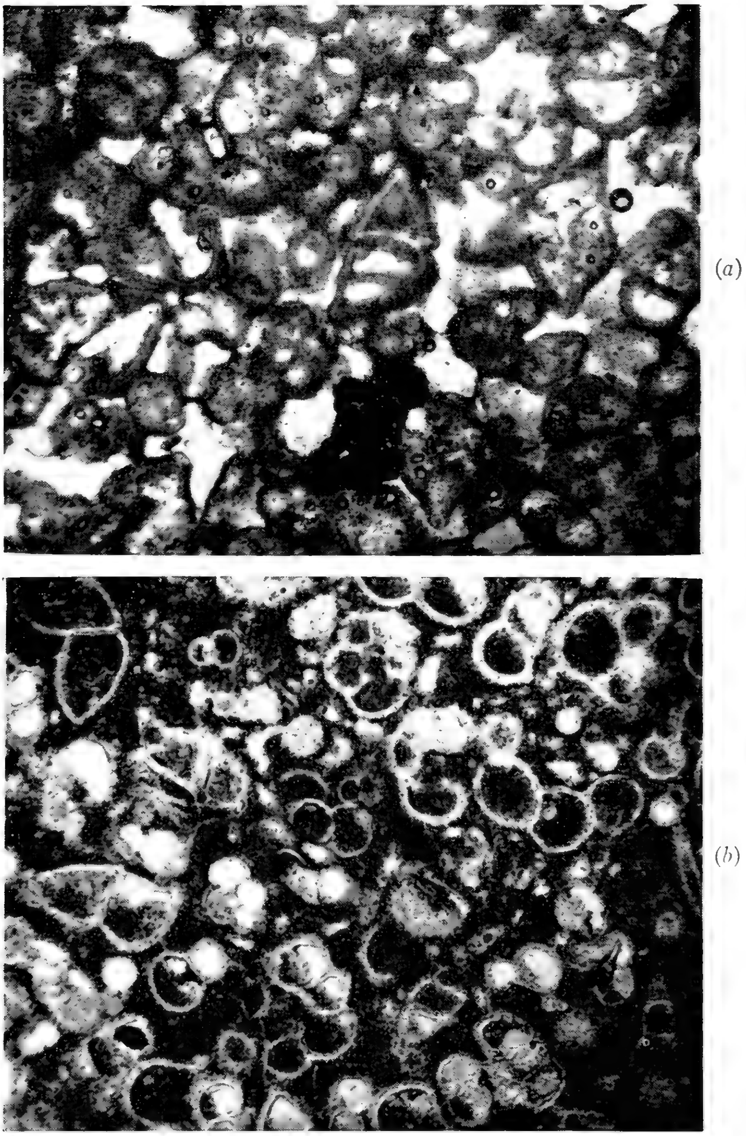


Fig. 6. Photomicrographs of thin sections of cemented Lower Tertiary foraminiferal limestone: (*a*) Sample No. 2, Mid-Pacific Station 26 A3, (*b*) Sample No. 5, Mid-Pacific Station 37 C. (approx. ×40).

TABLE III. Properties of Lithified *Globigerina* Ooze[a]

Sample No.	Density Solids, gr/cc	Porosity, %	Velocity, km/sec (±0.02)
1	2.70	68	1.77
2	2.87	62	1.95
3	2.83	24	3.86
4	2.86	12	4.75
5	2.85	5	5.46

[a] Based on samples taken on the Scripps Institution-U. S. Navy Electronics Laboratory Expedition in 1950. Velocities determined by the California Research Corporation at La Habra, California.

expect that the depth to lithification in a clay section and in a calcareous ooze section should be, in general, within the depth limits of 150 to 700 m, with an average depth around 300 to 400 m.

Almost everywhere there is a top layer of low-velocity material which lies, on the average, within the limits noted above. The work of Hill (1952, 1957), Hersey *et al.* (1952), Officer (1955), Katz and Ewing (1956), Nafe and Drake (1957), and others indicates that there is a fast changing velocity gradient to around 300 m, below which the gradient is less. Thus, refraction and reflection horizons commonly occur at depths from 400 to 800 m in Atlantic sediments (Nafe and Drake, 1957). In the Atlantic and adjacent seas Ewing and Ewing (1959) noted transformation to shear waves, and refraction and reflection horizons presumed to have taken place from semiconsolidated layers within the sediment column. In the Arctic Basin reflection arrivals are from depths of 250–300 m with average interval velocities of 2.04 km/sec (Crary and Goldstein, 1957). In the Pacific, in the northeast red clay area there is an average first layer thickness of 290 m, but in the east central Pacific calcareous area it is 330 m (Raitt, 1956). A reflection horizon also occurred in the same area at depths between 200 and 300 m (Shor, 1959). In all oceans investigated Gaskell *et al.* (1958) showed the presence, or probability, of a topmost layer of low velocity. In many areas there are thicker sections of 1 km or more recorded; in all but a few of these determinations the writers do not exclude the possibility of masked layers in the sediment column and further exploration may well show shallower reflecting horizons. The presence, in all the ocean basins, of a topmost layer on the order of 300 m in thickness is important evidence on the possible depths to lithification previously discussed and is probably the expression of a universally valid phenomenon.

Compressional Wave Velocities in Deep-Sea Sediment and Rocks

Unlithified Sediments

Until about 1954, very little was known about velocities in the surficial, unlithified sediments of the sea floor. Until that time, readable returns were not usually obtained from seismic studies, and, as a rule, velocities were assumed for these sediments. Within the past few years, however, studies by Laughton (1954, 1957), Nafe and Drake (1957), Sutton *et al.* (1957), Shumway (1956, 1958a, b), and Hamilton *et al.* (1956), plus the work at sea by the Lamont Geological Observatory, Cambridge University, Woods Hole Oceanographic Institution, and Scripps Institution, have indicated that these velocities vary with various physical properties between 1.43 and 2.12 km/sec. The velocities above about 2.0 km/sec indicate some degree of lithification.

Lithified Sediments

The general subject of seismic velocities in lithified sediments (sedimentary rocks) is of great importance in seismic exploratory work in the oil industry, and lately, due to seismic work at sea, the subject has assumed critical importance in our understanding of the structure and history of the ocean basins. As a result of this double interest there has been considerable laboratory and field work to determine the velocity of sound in sedimentary rocks.

The velocity of sound in rocks has been shown to increase with decreasing porosity, increasing rigidity, age, mineral constituents, and other factors. In shale there is a regular increase of velocity with depth (as porosity decreases) and with age (see, for example, Faust, 1951). For limestone, however, porosity variations considerably outweigh the influences of differing materials, pressures, and other environmental factors, as shown by Wyllie *et al.* (1956). The same authors (1956, p. 65) plotted an experimental average curve of porosity against velocity for limestone. The curve, representing, of course, an elongate area of data spread, is valid under differing conditions in laboratory and field, including oil wells where the estimated velocity from the porosity data compares favorably with the velocity as determined by the new, continuous-velocity logging technique.

In Fig. 7 note the positions of the five samples of deep-sea lime-

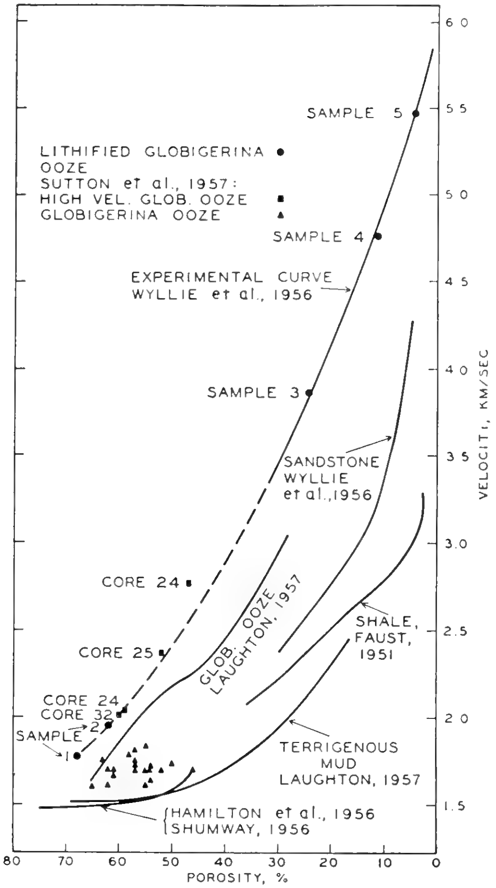


Fig. 7. Porosity vs. velocity of the elastic compressional wave in various sediments and rocks.

stone. With the curve of Wyllie *et al.* (1956) the velocity was predicted within less than 2% prior to the actual determinations. Randomly oriented calcite grains in a pure rock of zero porosity would have a velocity of about 6.8 km/sec, which represents the highest theoretical value for velocity in a limestone (Wyllie *et al.*, 1956). Field and laboratory data, however, show that the highest value normally to be expected should be about 5.9 km/sec, although a few velocities of the range 6.1 to 6.45 km/sec have been reported by Birch *et al.* (1942) and Hicks and Berry (1956).

Discussion

We are principally interested, here, in the actual field variations of velocity with depth (Fig. 8). Faust (1951), in his study of these

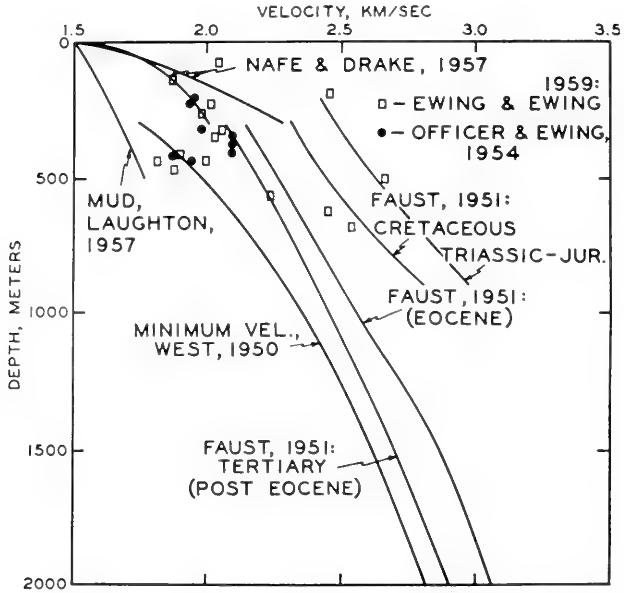


Fig. 8. Variation of velocity with depth. Shale sections (Faust, 1951; West, 1950) and unlithified sea floor sediments to 300 m (Nafe and Drake, 1957) compared with seismic refraction information of Officer and Ewing (1954) and Ewing and Ewing (1959). These field determinations are contrasted with laboratory experiments on terrigenous mud (Laughton, 1957).

variations for a large number of dominantly shale sections, utilized actual velocities from over seventy wells to form the Eocene and Tertiary (post-Eocene) curves. In these the velocity increases from about 2.1 km/sec at 300 m to about 3.32 km/sec at 3000 m. Because of the great amount of data involved, they can be taken as expectable variations of velocity with depth in Tertiary shale sections.

The previous discussion on consolidation, lithification, and velocities now permits us to predict the situation present in a noncalcareous, post-Cretaceous, clay section built up through a long geologic time span. Throughout geologic time, a sediment column, in an area of slow deposition, consolidation, and lithification, would have, at the top of the column, about the same thickness of unlithified material. It has been shown that this would ordinarily be of the order of 150 to 700 m with an average near 300 to 400 m. A natural consequence of this would be that the thickness of the lithified portion of the column would gradually increase while that of the topmost portion remained fairly constant.

At the surface of the sediment the velocity should be of the order of 1.5 km/sec (Fig. 8). The work of Nafe and Drake (1957) and others in deep and shallow water indicates that the velocity gradient will increase with depth so that at about 300 m the velocity is about 2.1 km/sec. Average velocity in the topmost, unlithified section will be of the order of 1.8 km/sec. At about 300 m there should be a conversion to shale (in line with our previous discussions). There should be a lower, lithified section of clay shale which varies greatly in thickness because it is being added to at the top by the relatively constant-thickness upper layer. In this lower layer the average velocity will vary according to the thickness of the layer, but will be near 2.1 km/sec at the top as shown by Faust (1951). It should be emphasized that these estimates are only for a clay-shale section—any calcareous material will cause the velocity to be higher.

Two papers almost ideally illustrate the foregoing possibilities. From studies by Officer and Ewing (1954) on the continental slope south of Nova Scotia it can be seen that the velocities are much closer to those expectable for a clay-shale section than for an unlithified section of terrigenous mud, as shown by Laughton's (1957) data, which have been converted from pressure to depth (Fig. 8). Ewing and Ewing (1959) give numerous examples of refraction and reflections at depths below the water-sediment interface. These horizons are supposed to be due to semiconsolidated sediment, and the foregoing analysis certainly bears them out.

Most of the previous discussion has been concerned with consolidation and lithification in a clay-shale section. Hypotheses, and the field data of oceanic seismic work, such as that previously noted by Crary and Goldstein (1957) in the Arctic and by Ewing and Ewing (1959) in the Atlantic, coincide very well in indicating the probabilities of depth to lithification.

If one grants that the highest velocity expectable in a shale section at relatively shallow sediment depths is less than 4 km/sec, then one has to explain the high velocities frequently found under some areas of present red clay deposition, as in the northeast Pacific. These velocities range from 4.5 to 6 km/sec (Raitt, 1956) (Fig. 9). In discussing the high-velocity second layers in the Pacific the evidence is much more speculative. If the first layer, alone, represents the entire sediment column, then there is, indeed, an anonomalously thin layer of sediment in the Pacific. The principal reasons advanced to explain this thin veneer of sediment have been: (1) the lower part of the sediment column has disappeared owing to some catastrophic cause; (2) the lower part of the column is undetectable by seismic means; (3) vast floods of lava or other volcanics were spread over the ocean floors; (4) the rate of deposition has been extremely low.

As previously noted, the more important factors governing depth to lithification in a calcareous section would normally be the same as those involved in lithification of clay into shale, namely pressure, chemical factors, and age. In areas of known calcareous deposition, for example, the east Pacific calcareous area, the first layer averages 260 m (variation from 200 to 340 m); in the equatorial area of maximum accumulation, three stations indicate a top layer of average thickness of 490 m [variation 380 to 570 m (Raitt, 1956)]. All these thicknesses are within the previously discussed general range of thicknesses to lithification;

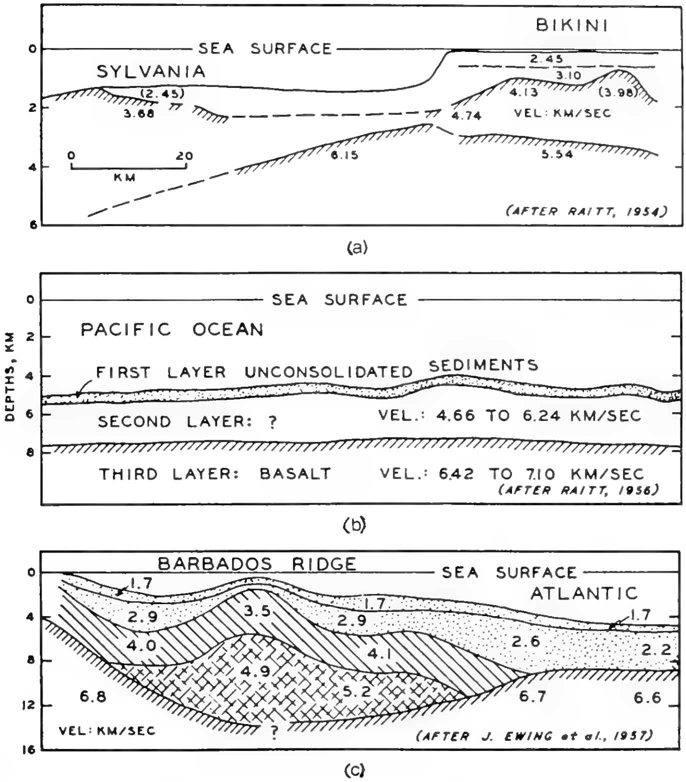


Fig. 9. Layered structure of the sea floor in selected areas: (*a*) N-S section through Bikini and Sylvania (Raitt, 1954); (*b*) diagrammatic structure in the northeast Pacific Basin (Raitt, 1956); (*c*) E-W generalized structure across Barbados Ridge (Ewing *et al.*, 1957).

the increased thicknesses under the equatorial current areas thus require no special explanation although increased rates of deposition are probably a factor because age is a factor in degree of lithification.

Geologic history indicates that the distribution of calcareous deposits during the late Cretaceous and early Tertiary were probably more widespread than today. This is especially true, as noted by Arrhenius (1952), in areas adjacent to present calcareous sedimentation. This probability, plus the discovery of high-velocity foraminiferal limestone previously discussed, indicates that the simplest supposition is that the high-velocity lower layers in the Pacific are composed of limestone lithified from oozes deposited during former times of calcareous deposition and now covered by unlithified calcareous ooze and red clay.

All previously noted alternative explanations for a thin veneer of sediment over high-velocity layers are possible and should be accorded proper consideration. Certainly in many areas, especially those adjacent to islands and seamounts, the best explanation for the high-velocity second layer is undoubtedly afforded by layers of lava. The section is undoubtedly complicated in many areas by fractured zones, pyroclastics, dikes, and sills; and metamorphism of sediments probably plays a part.

I should like to propose an alternative previously discussed. As a background, imagine the situation which might arise in an extremely ancient ocean basin which dates back at least into the Paleozoic or pre-Paleozoic. In an area where calcareous deposition is now taking place, the original deposits could have been clay, now lithified into clay shale (Fig. 10). During the Cretaceous, planktonic Foraminifera evolved and, together with coccolith ooze, began to form calcareous deposits which have been continuous to the present day. At depths of several hundred meters in the sediment this material, through pressure-induced chemical changes, has lithified into limestone of high velocity. The underlying clay shale would, of course, not be detectable by refraction surveys because it has a lower velocity than the material above.

In an area in which clay is now being deposited, as in the northeast Pacific, the first deposits could again have been clay, now lithified into clay shale. Above this material, during the Cretaceous, calcareous deposition began, but ceased sometime during the Tertiary under the influence of cooling bottom waters, as warm isotherms moved south. Geologic history affirms that these climatic changes actually occurred. Red clay deposition then continued until the present. At depths of several hundred meters in the sediment the calcareous material lithified into limestone (Fig. 10).

There is no reason to suppose that the material lithified at the

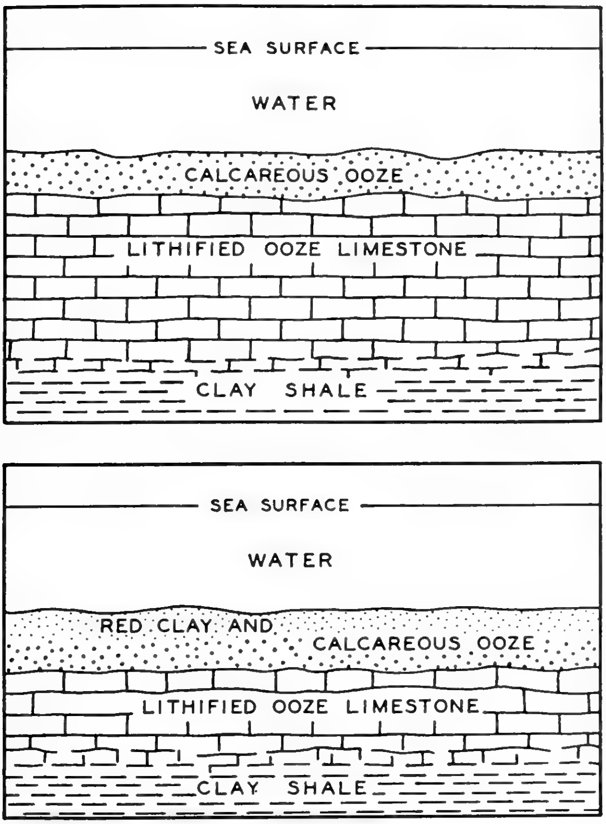


Fig. 10. Hypothetical sections of the deep-sea floor in the Pacific: (*top*) assuming a change from clay to calcareous ooze deposition which continued to the present time; (*bottom*) assuming changes in deposition from clay to calcareous ooze and back to clay which continued to the present time; possible lithification of the original materials to shale and limestone is indicated.

exact boundary between the clay now being deposited and the calcareous material of earlier times. Farther south we know that the upper sediments are unlithified calcareous ooze and that such material has been deposited for some time, as postulated by Shor (1959). In the northeast Pacific red clay area, coring by Scripps Institution has revealed unlithified calcareous ooze at shallow depths beneath the clay. Such a mixture of unlithified calcareous ooze and clay should have been deposited at higher rates than for clay alone, which allows time, since the Middle Cretaceous, for pure deposits of calcareous ooze to have been formed.

The view has been expressed that the second layer of high-velocity material cannot be limestone because the geochemical balance cannot tolerate that thickness and volume of calcareous material. As is well known by geophysicists, these high velocities are from the *top* of such a layer and have no bearing on the composition of the layer at depth. With this fact in mind it is no longer tenable to suppose that the second layer velocity cannot indicate limestone because of the geochemical balance. The total thickness of sediments and sedimentary rocks in an ancient ocean basin is likely, in many places, to be the total thickness of the upper unlithified layer and the lower, higher-velocity layers. In the northeast Pacific one result of this would be that the total thickness of the first and second layers should be thinner in the north and should progressively thicken toward the south to reflect the southward movement of warmer isotherms during the Tertiary, and higher rates of deposition in areas of calcareous depcsition. The calcareous surface should continue to dip to the north from its present outcrop area near the equator, which has actually been observed by Arrhenius (1952).

Volume of Sediments and Ages of Ocean Basins

Some of the other interesting results of applying soil mechanics concepts to deep-sea sedimentation and stratigraphy are in studies of the total volume of original sediments deposited in specific localities, the volume of solids present, and in studies of the ages of ocean basins. Standard soil mechanics computations allow the prediction of settlement in a sediment column provided the void ratios before and after consolidation are known (or estimated). Conversely, it is also possible to determine approximately how much sediment was required to consolidate to present thicknesses (Hamilton, 1959). The amounts of clay necessary to consolidate to present thicknesses are surprisingly large: 1000 m of original deposition will consolidate to about 500 m; it took more than 5000 m of clay to form a present consolidated section 2000 m thick.

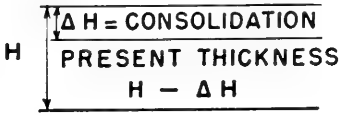
Table IV shows that much lesser amounts are needed for present thicknesses of calcareous ooze: only 565 m of original material are required for a 500-m consolidated section of calcareous ooze.

TABLE IV. Original Accumulation Necessary to Consolidate to Present Thicknesses

Depth Interval in Sediment, m	Present Thickness Increment, m	Original Accumulation for Present Increment, m		Cumulative Thickness of Original Sediment, m	
		Clay	Calc. ooze	Clay	Calc. ooze
0–100	100	155	105	155	105
100–200	100	190	110	345	215
200–300	100	205	115	550	330
300–400	100	220	115	770	445
400–500	100	230	120	1000	565
500–1000	500	1230	630	2230	1195
1000–2000	1000	2860	1385	5090	2580

The table is computed from tables illustrating consolidation and by using the following equation:

$$\Delta H = \frac{e_0 - e_f H}{1 + e_0}$$



where H = original thickness

ΔH = amount of consolidation

$H - \Delta H$ = present thickness

and
$$H = \frac{1 + e_0}{1 + e_f}(H - \Delta H)$$

where e_0 is the original void ratio, and e_f is the final void ratio. The relationship between void ratio and porosity is:

$$e = \frac{n}{1 - n}$$

where

$$e = \frac{\text{Volume of voids}}{\text{Volume of solids}}$$

and the porosity is:

$$n = \frac{\text{Volume of voids}}{\text{Total volume}}$$

In a paper on seismic refraction results in the Atlantic Ocean, Ewing and Ewing (1959, p. 296) show three stations (Fig. 11) in and near the abyssal plain (stations G-10, G-12, and G-13, located in the area 25° 23′ to 26° 25′ N Lat, 67° 26′ to 72° 02′ W Long; average water depth: 5.47 km). In this area there is an average of 320 m of sediment (velocity 1.70 km/sec) overlying second layers with an average velocity of 2.16 km/sec (at the top of the layer), and an average thickness of 883 m. These velocities and thicknesses indicate a probable clay-shale section. If this is a

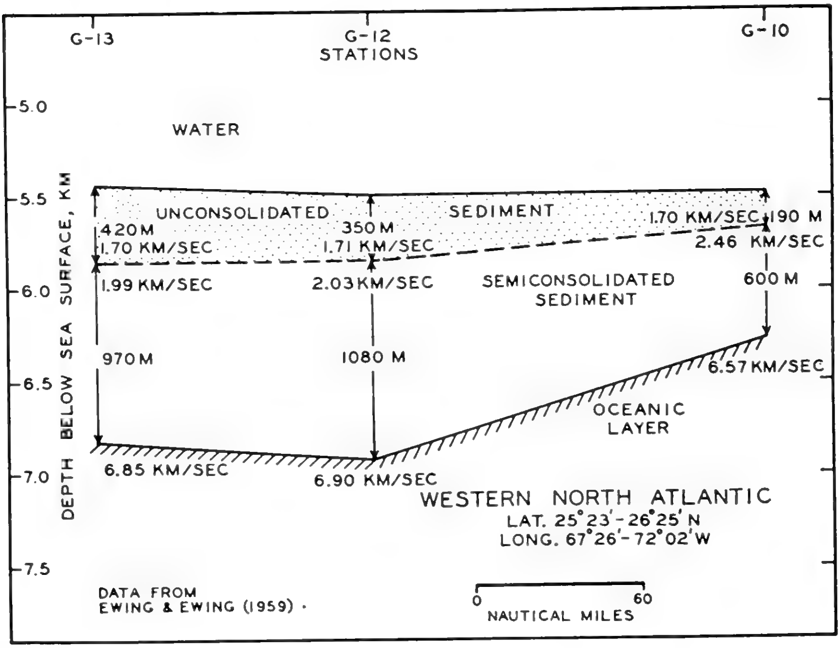


Fig. 11. Seismic refraction survey results from the Western Atlantic Basin (Ewing and Ewing, 1959).

clay-shale section, it required about 2780 m of material to consolidate to the present average thickness of 1203 m.

In the northwest Atlantic abyssal plain, Ewing and Ewing (1959) record a first layer thickness of 440 m (velocity 1.62 km/sec) overlying a second layer of 1090 m thickness with a velocity of 1.82 km/sec at the top of the section. If this is a clay-shale section, it took about 3690 m of original deposits to consolidate to the present thickness of 1530 m.

The hypotheses, calculations, and measurements previously discussed allow some generalized calculations of the amounts of solid materials at any specific locality. If a general assumption is made that the average porosity of all the original deposition was 70% (or 30% solids), then the following amounts of solids would be present in the sections just discussed:

1. In the western Atlantic (at The Lamont Observatory, see Fig. 11, stations G-10, 12, and 13), where the total sediment column averages 1203 m thick, and calculations predict a total amount of deposition of about 2780 m, there would have been about 840 m of solids in the section.
2. In the northwest Atlantic abyssal plain where the sediment section is 1530 m thick, there should have been about 3690 m of original deposits; here the solids should total more than 1100 m in thickness.

It can be seen that, even with a conservative estimate for the amounts of solids in the original section (30%), the total amounts of solids in the layers above the basalt, for these areas, fall close to the estimated thickness of solids (1 to 3 km) postulated by Kuenen (1950) and Revelle (1954) as necessary to supply the materials indicated for the geochemical balance.

Ages of Ocean Basins

Obviously we have here an interesting method of estimating ages of ocean basins if only valid rates of deposition were available. Broad generalizations about ancient rates of deposition in the deep sea have little validity at the present time, but it is apparent that *present* rates vary between 0.4 to a little over 1 cm/1000 years for calcareous material and from 0.05 to 0.5 cm/1000 years for clay. These ranges might be used as a first approximation in estimating time in thickness computations. After computations have been made of the amounts of original deposits in any specific locality, the application of any generalized rate of deposition will yield an estimated age for the deposit.

Obviously any age computations based on these rates are nebulous in that ancient rates of sedimentation are, at best, only poor estimates. The results of this method, however, when applied to various localities, fall into the category of evidence which indicates ancient age of the ocean basins, namely Paleozoic to pre-Paleozoic.

Summary

A very important job is to be done in computing the volume of sediments presently in the ocean basins of the world. To do this properly it will be necessary to have at hand a much more comprehensive seismic survey coverage of the ocean basins; the surveys will have to be classified by environment into basins, ridges, continental shelves and slopes, and similar areas which contain varying thicknesses of sediments owing to their location and sedimentary history. It must also be decided whether or not the lower layers are the lithified equivalents of the upper layers and/or other different sediments deposited under different conditions.

The concepts of this paper will not apply to all sections measured seismically in the oceans. As more and more evidence is derived about the sea floor, we realize that generalizations are likely to be untenable. Near volcanic islands and ancient drowned islands, the sediments of the archipelagic aprons are likely to be thick and composed of pyroclastics, erosional debris, lava flows, and clay and organic material settling from the upper waters. The seismic picture is undoubtedly complicated in many areas by volcanic effusions building up into seamounts, seaknolls, or intruded into the sediment column. Fractured zones and areas of slumping and lack of accumulation are further complicating problems. Some areas may contain sediments and rocks metamorphosed at depth. The caution at this point is that each area must be studied as an entity.

The thickness and composition of the sediments of the deep-sea floor will never be exactly known until holes are drilled in selected areas; until that time we can use only the best indirect evidence available and consider all alternatives. The project to drill through the layers of the deep-sea floor should be strongly supported.

The thickness of sediments in an ancient deep-sea basin is likely to be the total thickness of the upper "unlithified" layer and lower, higher-velocity layers, in short, the total thickness of all layers above the presumed basalt. A measurement of sediment thickness at any time horizon of the past, or future, should show about the same value for the topmost part of the slowly consolidating sediment. The presence of an intermediate velocity layer between the unlithified sediment and the basaltic basement rock can thus be explained in many areas as normal expected consolidation and lithification of the present types of sediment in an ancient ocean basin. If this is true, the geochemical balance calling for large amounts of solids on the sea floor, recent seismic discoveries in the ocean basins, and the consolidation theories of soil mechanics engineering fall approximately into line.

One of the results of deep-sea exploration, especially deep holes bored through the sedimentary layers, will be the production of columnar sections showing the sequence, interrelations, and thicknesses of sedimentary units. When enough of these sections have been produced, the study of the stratigraphy of the deep-sea floor will yield the last, missing data which will permit the writing of a first valid geologic history of the whole world. We must hurry because we are faced with unraveling the geology of other planets before we have unraveled that of our own!

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The Biologist Poses Some Problems

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THIRTY years ago the role of a biologist in a symposium of this kind would have appeared both simple and illuminating. Macallum's (1926) ideas on the chemistry of the blood of freshwater vertebrates were widely accepted, the huge span of pre-Cambrian time was unappreciated, so that the earth appeared much younger than it does now, and the obvious conclusion that by analyzing the blood of teleosts we could get the composition of the middle Paleozoic seas remained unchallenged.

In 1931 Pantin published a skeptical essay on the matter, and in 1942–43 came Conway's fundamental papers which demolished completely the older views. Conway (1942, 1943) showed that at least throughout Phanerozoic times there can have been very little change in the concentration of the major ions of sea water. Only in a few cases, notably in that of strontium, can we hope for direct evidence of ionic ratios, and even in this one case there is considerable uncertainty among different investigators as to whether a significant change has indeed taken place. The indirect arguments used by Conway, however, seem so compelling that in the absence of any clear contrary evidence we may assume that during the period for which we have good fossil evidence the sea has remained very much the same in overall chemical composition.

The differences between sea water and cell or body fluids appear now to be related in part to the evolution of various biochemical mechanisms in which ions have a function, and in part to the history not of the ocean but of animals which can migrate from salt to freshwater and back again. It might, therefore, appear that the biologist has little to offer even in the process of framing suitable questions. My hope is to show that with a little patience and insight this is not really the case.

In order to investigate the matter it is, as I have just indicated, necessary to have patience, for we shall first have to examine rather closely the problems of the classification and so implicitly the phylogeny of living beings, and this is a matter that usually appears uninteresting to those people who do not find it of interest.

Enormous advances in the study of morphology have taken place during the past two decades, largely as the result of the development of the electron microscope.

It is now reasonably clear that surveying the whole of animate nature, we can make a fairly good initial dichotomy into those organisms which lack a multistrand flagellum, true mitochondria and chromoplastids, and those in which one or more of such structures are found.

For the first group we may use, following current practice, if not strict priority of usage, the term Monera, and regard the group, following an old convention in nomenclature, as a kingdom. The Monera are presumably divisible into at least four major groups. Of these the Eubacteriae and Spirochaetae are essentially swimming organisms, to use Pringsheim's (1949) convenient term, in which a flagellum quite unlike that of the members of the higher kingdoms may be developed. The Myxophyceae and the Myxobacteriae are in contrast gliding organisms. Some modern authorities (e.g., Stanier, 1959) are clearly on the point of making two phyla, one for the swimming and one for the gliding forms, but no names have been given. There is unfortunately nothing to hint which group is the more primitive. Also some organisms are still *incertae sedis* and are hard to discuss briefly because they seem to lack properly established names. The most important form a group including the causative organism of bovine pleuropneumonia, *Asterococcus mycoides*. Apparently allied to this is a very distinguished type of organism originally isolated from sewage by Laidlaw and Elford (1936) and subsequently found in soil (Seiffert, 1937), which has been called, though perhaps invalidly, *Sapromyces laidlawi* Sabin. It is of immense theoretical significance because it is apparently the smallest free-living organism yet known, having during the early part of its life history a diameter of the order of 100 mμ. Some microbiologists regard these organisms as degenerate Eubacteriae, others place them as an independent group.

When we consider the broad environmental requirements of the Monera we find that in general they are organisms living at solid-liquid or liquid-gas interfaces in a great variety of circumstances, in soils, aquatic sediments, on suspended tripton, or as epiphytes, commensals, symbionts, or parasites. Only in the photosynthetic groups do massive populations develop as plankton in the free water. On the whole, the major groups show little specialization into freshwater or marine organisms. In many genera in the Eubacteriae and the Myxophyceae and in some of the few genera of the smaller groups marine forms occur and these are often easily adapted, apparently by an evolutionary process involving few mutations, to freshwater or very euryhaline life. Specific marine genera occur only in a few orders, such as in the Pleurocapsales among the blue green algae, and these are not primitive. So far organisms like *Sapromyces* appear to be known only from nonmarine environments, though various problematic fouling organisms are recorded from the sea, some of which may prove to be very unspecialized. Any genus containing both fresh and salt water species is obviously able to go from one environment to the other by a series of genetic changes not greater in number than is required to make a species. Within the bacteria many cases are known from the monumental work of ZoBell (1946) where such changes take place over a quite short period of time, presumably within the species. Little is known of the physiology of the processes involved in genetic adaptation of this sort, but the work of Pratt and Waddell (1959) suggests that ultimately much can be learnt of the mechanisms involved. All organisms within a restricted taxon showing this kind of diversity will be regarded as exhibiting *evolutionary euryhalinity* to a greater or less degree.

We are evidently justified in concluding that evolutionary euryhalinity is characteristic of a great variety of Moneran lines. Where there is a suggestion of a more stenohaline history it is reasonably certain that the sea is not more favored than nonmarine environments; possibly it is less favored.

When we leave the Monera we find great difficulty in deciding how the majority of described organisms should be classified. It is reasonable to assume with Dougherty and Allen (1959) that the red algae are the most primitive group of higher organisms, and that the Cryptomonadineae relate them to the rest of the Protista. From some ancestral unicellular biflagellate that must have been near the ancestor of the existing Chrysomonadina a large number of lines have presumably radiated, giving rise to the brown algae, dinoflagellates, diatoms, aquatic fungi, and through the zooflagellate groups, the animal protista. From some group or groups in the last the multicellular animal forms have originated. The green algae and all the terrestrial green plants presumably come from isokont green flagellates whose relationship with the other plant flagellate groups is problematical.

When we consider the various lines, or to use Huxley's convenient term, *clades* of the higher organisms, from the standpoint of what I have termed evolutionary euryhalinity, the results are striking and very interesting.

In the red algae, in the lower class, the Bangioideae, and in the Nemalionales, the lowest order of the higher class of Florideae, we find a mixture of salt water, freshwater, and euryhaline forms living both in water and soils. In the higher orders of the Florideae, with the single exception of one or two members of the genus *Hildenbrantia*, all the species are marine. The lower red algae are thus ecologically comparable to the Monera in exhibiting considerable evolutionary euryhalinity, whereas practically all the higher forms are stenohaline.

In the Cryptomonadineae there is evidently much evolutionary euryhalinity. *Rhodomonas* has both fresh and salt water species. The same is true of the motile Chrysophyceae. From somewhere near the latter the brown algae must have evolved, and in so doing followed the pattern set by the red. The lowest order, the Ectocarpales, have both marine and freshwater members, but all the higher forms are marine. Much evolutionary euryhalinity is retained by many genera of diatoms, but others have become specialized to particular ranges of chemical composition, salt or fresh, acid or alkaline. The Dinoflagellates are largely but of course not exclusively marine; they seem to spring from a primitive family, the Desmomonadinaceae, which has obvious evolutionary euryhaline characteristics. The green algae show both fresh and salt water branches, but the terminal groups seem either one thing or the other, while the lower groups retain much evolutionary euryhalinity. The same situation certainly is reflected in the less well documented evolution of Foraminifera. In view of the general lability of all the lowest protist groups we may expect a similar history for the purely marine but very specialized Radiolaria and Acantharia.

If we adopt the Hadzi-Hanson type of phylogeny for the metazoa, marked evolutionary euryhalinity is retained by the ciliates into the lower flatworms; if we adopt the more conventional Haeckel-Hyman theory of a coelenterate ancestry, the evolutionary euryhalinity is lost by the time the metazoa appear. Thereafter we have in the animal kingdom great lineages of marine forms, with occasional production of limited groups capable of invading freshwaters. In the higher forms this occurs in a very superdispersed way. Almost all the cases in the Polychaeta, for instance, are in the *Nereidae* or *Fabriciinae* as Hartman (1938) points out. A single invasion into freshwater from the whole range of deuterostome phyla is all that is certainly needed to explain the early habitats of the vertebrates, but this implies much migration backwards and forwards after a freshwater fish fauna was well established. Parenthetically it appears to the present writer that the evidence for a freshwater origin of the vertebrates per se is quite unconvincing. If that marvellous but almost completely ignored fossil *Ainiktozoon loganense* Scourfield (1937) is what it looks like, namely, a late surviving missing link between the tunicates and the true vertebrates, it certainly does not indicate a rheophil type of organization, but rather something living pelagically like a salp or *Velella* but with additional directional mobility. This mode of life would accord with the presence of a number of specimens in the *Ceratiocaris* horizon, presumably blown inshore into a lagoon, just as I have observed *Velella* blown up the artificial channel that connects Lake Avernus, west of Naples, with the sea.

If we now try to interpret the data presented by the general picture of salinity requirements against the background of modern classification, the simple conclusion would be somewhat as follows.

The earliest complete organisms lived in more or less interfacial habitats of low but perhaps somewhat variable salinity. This type of habitat remained the important one during the evolution of all the Monera. Terrestrial as well as freshwater forms developed during this phase, but a wholesale invasion of the oceans of such a kind that could produce a specialized marine biota was delayed until relatively late, and coincided with the elaboration of cytological organization of the sort found in the Protista and higher plants and animals.

This hypothesis is put forward merely as the simplest one apparently concordent with the facts. The main objections that can be raised against it are that it implies that the modern ecology of organisms is comparable to their paleoecology.

There must be good physiological reasons for the apparent extreme superdispersion of invasions by marine metazoa into fresh waters. It may appear, since it is reasonably certain that no organism could work if the cytoplasm contained the same concentrations of major anions and cations as its medium, that some regulation across the bounding membrane was essential right from the beginning. Perhaps, therefore, the evolutionary euryhalinity of the Monera is what one should expect. Yet enough cases are known of large groups of Protista being exclusively marine to suggest that there is some adaptive meaning in the development of such lineages even when we are dealing with single cells, so that even if euryhaline adaptability is physiologically essential in really primitive organisms, we still have to explain why at a certain grade of evolution it tends to be lost.

The time relations of all these processes raise the second of the two problems that I want to consider, namely the very obvious one as to why the fossilized remains of animals are almost absent up to the Cambrian and then appear in great numbers. This matter will be discussed by a number of other specialists. My aim is merely to delimit the problem in a biologically significant way.

It is first necessary to realize that the appearance of skeletons does not imply the appearance solely of calcium carbonate skeletons. Although most skeletons in the Cambrian, as today, were certainly built of that useful substance, there were also calcium phosphate skeletons, as in the ecardinate brachiopods, and quite likely in some Trilobites and Aglaspida. Moreover, the first really certain siliceous organisms, the sponges and Radiolaria, appear about the same time. Claims have been made of radiolarians and sponge spicules in the pre-Cambrian, but they are not regarded as acceptable by most modern authorities on the groups (Raymond, 1935). Moreover, the general organization of the hard parts of the lowest fossilized arthropods clearly indicates that there must have been a considerable amount of organic matrix in the exoskeleton, and we know from the Burgess Shale deposits that during the middle Cambrian there was a vast fauna of arthropods with organic exoskeletons, strong enough to permit muscle attachments, but not heavy enough, or sufficiently mineralized, ordinarily to fossilize. It has often been supposed that the appearance of fossilizable skeletons in the lower Cambrian must reflect changes in chemical composition of the ocean also occurring at that time.

Phosphate is a very minor constituent of sea water and is an essential element in all organisms, whereas calcium is probably essential for all animals if not for all organisms, so that efficient mechanisms for collecting both calcium and phosphate would be early evolved. From these facts it seems extremely likely that calcium phosphate skeletons, if they had been desirable, could have been evolved under conditions of considerably lower calcium concentration than occur in the modern ocean, while the apparent contemporary introduction of siliceous skeletons at the same time as that of calcareous skeletons can have no simple geochemical explanation. For this reason it seems better to look for a biological explanation rather than one based on geochemical considerations.

When we examine the lower Cambrian fauna as a whole, the impression is very strong that practically all the organisms *known* to be present were microphagous, feeding either on detritus or minute organisms in sediments or on plankton. The mollusca presumably had radulae, since *Neopilina* has such an organ, but it is unlikely that such radulae were very effective organs of predation except possibly on any unskeletonized sponges and archecyatheans as may have existed. On the whole the known fauna gives the impression of an assemblage that could have got on well without skeletons. In the absence of predation it is probable that a heavy skeleton denser than sea water would always be an encumbrance to a marine animal. Cloud's (1948) view that skeletons are needed for muscle attachment has obvious merit, but the heavy type of skeleton that fossilizes well must go far beyond such needs, as is evident from the existence of an animal such as *Marella*, with as complex a set of appendages as a trilobite, but with a skeleton only fossilized under the exceptional circumstances of deposition of the Burgess Shale.

It is therefore difficult to avoid the conclusion that the rise of *fossilizable* skeletons implies the rise of predation, and that this affected animals of many different sizes at about the same time.

Since we find no evidence of powerful predators among the known lower Cambrian fossils, we only can assume that the predators did not fossilize. The most reasonable hypothesis as to their nature, implied rather vaguely by Raymond, would be to suppose the presence of protonautiloids perhaps with feeble conchiolin shells but quite powerful schleroprotein or horny jaws, cruising about just over the bottom. Some of the contemporaneous polychaetes would also probably have had well-developed jaws. What we know about the existence of nautiloids and polychaetes in the earlier part of the Phanerozoic record would practically compel us to assume their existence in an unfossilizable form in the lower Cambrian; the only really hypothetical part of the hypothesis is the postulation of jaws.

Current biological knowledge would therefore appear to be consistent with the existence of a relatively modern type of ocean well before the Cambrian, with no inevitable geochemical break at the opening of the fossil record. The events supposed to bear witness to such a break can be much better explained on biological grounds.

Much further back the facts that I have reviewed earlier would not be inconsistent with the emergence of the earliest complete organisms in quite shallow pools, wet rocks, or damp sediments on the growing continents, under conditions of low and variable salinity. From such localities the true ocean may have received its biota in the earlier stages of its development. This is indeed the simplest hypothesis that we can put forward on purely biological grounds. It may prove to be a hypothesis of low survival value. Something like it was suggested by Chamberlin (e.g., Chamberlin and Salisbury, 1904, p. 627) over fifty years ago, and again by Macfarlane (1923). To the majority of you, as oceanographers, it may seem merely the warped production of the brain of a limnologist. Time and the other papers in this volume may well show that I am wrong.

[*Note added in proof.* Since the above lecture was delivered, I have learnt that the hypothesis of predation as the stimulus to the production of hard fossilizable skeletons had already been put forward by Dr. Harold K. Brooks in a paper that has apparently not yet appeared.—G. E. H. 28 June, 1960.]

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Origin of Life on the Shores of the Ocean

Physical and Chemical Conditions Determining First Appearance of Biological Processes

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THE general account which I shall give here of the origin of life on the shores of the ocean is an attempt to picture only the very earliest stages of the origin of life, that is, those which mark the transition from the inorganic to the organic. I shall not attempt to discuss the complicated biochemical problems of the later stages in the origin of life, the origin of the genetic apparatus, of the cellular organelles, or of cells themselves. Consequently, this will be essentially a simple account, where I shall link what we know from physical oceanography about oceans and their shores, with what we know from geochemistry and geophysics. To see this in its setting of the whole process of *biopoesis* or life-making I would, however, like to summarize the picture I have of the process as one divided into stages. This is shown more or less arbitrarily in Table I, which is modified from that presented two years ago at the Symposium on the Origin of Life in Moscow (Bernal, 1959).

I distinguish seven logical stages in the origin of life which are shown with corresponding features in the external environment and in the molecular developments inside the pre-organismal seas and in the organisms that arose from them. The first stage is the proto-organic phase, when the smallest organic molecules such as amino acids, purines, and sugars are being synthesized from the inorganic molecules H_2O, CO_2, NH_3 occurring in the original hydrosphere and atmosphere. The second stage I envisage as the concentration of some of the more complicated molecules into

TABLE I.

Stage	Main New Constituents			Primary Free-Energy Source
	Surface of lithosphere	Hydrosphere	Atmosphere	
1. Production and concentration of simple molecules	SiO_2 Sand $AlSiO(OH)$ $Fe(OH)_2$ Clay $CaCO_3$ Precipitated limestone	NH_4HCO_3, H_2S, $NaCl$, KCl, KH_2PO_4 } Low concentrations	CO_2 (or CH_4) N_2 NH_3, H_2S, H_2O } Very little	$2NH_3 \rightarrow N_2 + 3H_3$ $N_2 + 2H_2 + 2H$ $8SH_2 \rightarrow S_8 + 8H_2$
2. Dehydrogenation and condensation. SUBVITAL AREAS	Same with FeS	NH_4HCO_3, H_2S, KCl } Decreasing concentration $NaCl$ Increasing concentration	Increasing N_2 Decreasing CO_2 CH_4, NH_3 and SH_2 disappear	Short-wave sunlight ?
3. Polymerization and coacervate formation EOBIONTS	Organically formed FeO(OH) and $CaCO_3$	K ions and inorganic PO_4 ionsdecreasing	Very low concentration of CO_2	Visible sunlight Metal clathrate photosynthesis?
4. Nucleoprotein organelles	Organically formed accelerated weathering	Composition approximating to present but less NaCl	Rapidly increasing O_2	Activated porphyrin PHOTOSYNTHESIS
5. Lipid-covered organelles	The same	The same with increasing NaCl	Atmosphere approximating to present composition	Lipid plastids with chlorophyll for photosynthesis
6. Membrane-enclosed cells Protobacteria ORGANISMS	Organic soils on land areas	The same with increasing NaCl	The same with increasing NaCl	Oxidation of S and Fe with atmospheric oxygen
7. Nucleated cells PROTOZOA	Trapped organic matter in sediments Oil	The same with increasing NaCl	The same with increasing NaCl	Separation of photosynthetic plants from organiphagic animals

Stages in Biopoesis

Developments in Biosphere						
Free-energy sink	Leading types of metabolism	Main metabolites	Coenzymes	Catalyst or Enzymes	Coherence Mechanism	Reproduction Mechanism
$CO_2 + 4H = H_2CO + H_2O$ Fixation of CO_2	CO_2, NH_3 condensation	NH_4^+ $CO_2(OH)^-$ CO_2NH_2 HS^-	$PO_2(OH)_2^-$ $\{PO(OH)_2\}_n$ Polymetaphosphoric acid	SiO_2 ?	Nonturbulent areas Sea bottoms Sand banks	None
The same	Dehydrogenation	Amino acids Trioses	$NH_2CO\ PO_2(OH)$	Clay Iron hydroxides	Adsorption on clay	Continuity of subvital areas
Primitive photosynthesis $2H_2S \rightarrow 4H + S_2$	Anaerobic fermentation	Peptides Pyrimidines Purines Pentoses	Proto nucleotides Flavones	Peptide protoenzymes	Coacervate drops of large peptide molecules	Simple division Evolution and reproduction not distinct
$2H_2O \rightarrow 4H + O_2$ Photosynthesis, liberation of oxygen	Formation and fermentation of carbohydrates	Proteins Nucleic acids Starch	ATP RNA	Protein enzymes	Protein-covered organelles in coacervates	Precise copying of nucleoproteins
$(n + 1)CH_3COOH \rightarrow CH_3(C_2H_4)_nCOOH$ Lipid formation	Oxidation of carbohydrates	Lipids Sterols	DNA	The same	Lipid-covered vesicles, spherical and laminar	The same
Maintenance of ionic concentrations	—	Cellulose	The same	The same	Lipid-based cell membrane	Fission and conjugation of nucleoproteins
—	—	Fibrous protein Myosin Collagen	The same	The same	Nuclear membrane Protein-covered cell wall	Mitosis and sexual reproduction

what I have called subvital areas, which I believe to be a form of adsorption on clay particles in estuaries. The third stage is that of polymerization and the formation of independent, purely organic, *coacervates* without mineral support. These are what Pirie has called the "eobionts." In the fourth stage we have the appearance of what are called organelles, composed of nucleoprotein. After that follow the fifth, sixth, and seventh stages, of more advanced organelles with membranes leading to the nucleated cellular organisms of the type of present day life; I shall not discuss these in any detail.

There are quite sufficient problems to be dealt with in the early stages to occupy scientists of a large number of disciplines for a long time. The general principles I have tried to use in working out the origin of life are those which have been used with success in all the previous attempts at establishing *origins* at different levels of organization from galaxies to human societies. The first of these is essentially the same as the uniformitarian principle used in the first place by Lyell in his analysis of geological phenomena, namely, as far as possible, by treating the past as if it were a backwards extension of the present. It means that, except when we have positive reasons not to believe it, we must imagine that the same kind of phenomena that occurred in the past occurs now, and then trace their possible consequences.

The second principle which I feel should be used is that introduced by Henderson (1913) in his *Fitness of the Environment*. This is that the subsequent stages of complicated systems make use of the inherent properties of those simpler stages already present. Life, which is built out of the substance of the classical elements of water and air, consequently makes use of the particular forms and properties of those substances. This, for instance, limits life for practical purposes to the region between 0°C and, say, 80°C, with a maximum somewhere in the region of 30° to 40°C. The special functions which are played in life by some ions and atoms, especially those of potassium, phosphorus, sulfur, and iron, depend not only on their being quantum mechanically adapted to these functions but also on the actual abundance of these atoms in the primitive ocean.

Now, with these considerations one can proceed to build a picture of the world without life which would lead rationally on to the occurrence of living processes. First of all, however, I should say something to modify previous views of my own and of others as to the dates of these stages. In Table I the stages are just put in logical order, and they are not attached to any particular dates but I have in the past imagined that the closing dates, so to speak, of number seven, the first definite organism, must be well before the base of the Cambrian, and indeed well before the appearance of anything that could be called a fossil in the pre-Cambrian. Let us take, therefore, a final date of about one billion years before now. If we consider the time required for the very complicated organic processes in the early stages of life and remember, further, that the evolution of life all the time we have known it has been going on at an accelerated pace, we must imagine that the early stages took a very long time. I had given them another billion years, placing the origin of life, let us say, between two and three billion years ago. I have now come to the conclusion that the origin of life may be considerably earlier. It may even antedate any of the rocks that we have on the surface of the earth today, even in the most ancient parts of the Archean, that is, dates of the order of three to three and a half billion years. I base this idea on the observations of the geochemists who have shown that fundamental types of rock, such as granites and gneisses of the oldest shields, have been formed from clay rocks derived from the detritus of earlier rocks. It is something of a puzzle that we do not see on the surface of the earth any rocks older than three billion years. To explain this I have formed a theory, which is much reinforced by the evidence brought forward at this congress, on the nature of the mid-oceanic ridges and the great lineations in the Pacific. My belief is that what we observe in the earth's crust may be only the later stages of a process of what might be called revolutionary movement in the crust, in which new crust is formed in the centers of oceans and is gradually pushed over to create new continents and then is pushed under again and destroyed (Bernal, 1959; Blackett, 1960). The motive force for such vast changes I find in subcrustal convection currents.

But however this may be, the probability is that living processes are very early, and this quite apart from still disputed evidences of early Archean fossils, for the elementary reason that no sure evidence has yet been found for any differences between the surface geochemical processes occurring at the earliest dates accessible to us and those that occur today. And this, despite a certain amount of rather doubtful evidence from isotope distribution, would seem to indicate that we have plenty of time, I should say about three or four rather than one billion years to account for the origin of life.

Of course, what I say may be upset at any time if new evidence comes forward from other isotope studies as to a regime in rock formation, particularly in regard to the state of oxidation of iron and sulfur which would seem to indicate a different regime; but until this does come, I think we would be on safer ground in pushing back the origin of life as far as we can. The absolute date does not matter so much. The essential is that there should be time enough for the formation of the basic chemicals out of which living systems are formed.

In my opinion the major difference between the early stages and the present is the comparative absence of the hydrosphere or the oceans. The evidence presented at this congress seems to indicate that the earth's crust has undergone a very considerable degree of reworking over the known part of geological history, and, if I am right, also over a long preceding period. The result of this must have been the liberation of a great deal of water from the lower parts of the crust and even the of mantle of the earth. I believe the mechanism for this is very deep seated, at least as deep seated as the deep focus earthquakes, say 700 km down. Here, as we now understand, the rocks are not of the familiar crystalline types but must be of an ultradense type; for example, the olivine of most of the basic rocks is converted into a spinel. All these rocks contain a considerable amount of water and nitrogen, and this will be liberated gradually by the orogenic processes that have taken place in various cycles, possibly as many as sixty cycles, since the first formation of the crust.

This would mean the gradual growth of oceans, not as rapid as the rate of liberation of water into the atmosphere through volcanos, but nevertheless more rapid than the trapping of water in sediments, so that there will be a net gain over the geological periods and a continually deepening and probably also widening oceans. The composition of this ocean will also be liable to change, but, if it is also growing, the change will not be as much as it would have been if the ocean had originally had its present volume. That means that a smaller absolute amount of dissolved substances would produce a greater concentration. The evidence, as I see it, is that the present concentration of sodium chloride in the oceans is relatively recent—the result of a progressive process of enrichment. The early oceans may have contained less sodium, not only relative to the water but also relative to the potassium. I base this on indirect evidence from the potassium content of living organisms which is high compared to ratios found in sea water. But, as will be seen later, this may depend also on the relative absorptions of sodium and potassium ions by clays.

However, the major constituent which was liberated along with the water into the early atmosphere must have been carbon dioxide. It is argued that carbon dioxide is too oxidized a form to be the basis of living structures and, indeed, there may be even deeper down a certain amount of more reduced substances; the presence of diamonds in the deepest pipes indicates that such things do exist. Nevertheless, I believe that a spinel-like form of olivine could contain carbon in place of silicon; it would effectively be an orthocarbonate, stable at high pressures, but one in which carbon dioxide would be liberated by any movement which disrupted the old complex or brought it nearer the surface. Some evidence of this is furnished by the carbonatite rocks of very ancient origin. The evidence from present day volcanos indicates that CO_2 is the major volcanic gas after steam, and only some of this is likely to be of secondary origin derived from corals or limestones. This leads me to modify the views expressed by Oparin and also by Urey as to the composition of the early atmosphere, which I feel is likely to have contained relatively little hydrocarbons, more carbon dioxide, and a certain amount of ammonia or nitrogen produced by its decomposition. In other words, my own views have been influenced by those of Rubey (1955), but here I have less right to talk than others more expert in physical chemistry. The point I want to make later is that the precise composition of the early atmosphere is not of decisive influence on theories of life, except in one respect: the relative importance of photosynthesis at the different stages of the evolution of life. If we start with less energetic compounds, we need to evoke the energy of photosynthesis at an earlier period.

The significant elements to be found on the primitive earth or its hydrosphere, were essentially the simple ions of potassium, sodium, magnesium, and calcium, a certain amount of phosphate, though relatively little on account of its insolubility, as well as iron and sulfur compounds, possibly reduced. These, according to Henderson's principles, would be the natural basic materials which would come together to make life possible. Certainly their special properties, particularly the sulfydryl-sulfur and ferrous-ferric oxidations and the coordinating power of transition elements such as iron, cobalt, copper, and nickel, suggest that the first stages in preparing the evolution of life were really in the nature of the working out and combining of the properties of the substances that were there at the outset.

Now, a geological-geochemical system of the type I have just described should be considered as approximately but not absolutely in equilibrium. If it is in absolute equilibrium we would not have to discuss at all problems like the origin of life—it would have gone on indefinitely without any more complication. It is only a slight trace of instability in the system that could lead in one direction to the formation of more complicated compounds. We have, in fact, two problems to face in the origin of life; the first is how were the compounds which at present characterize life first formed and by what stages; and the second, how did the chemical mechanisms which we now recognize as metabolism originate? In other words, we can ask ourselves how, within a certain volume, self-contained chemical processes could be established and balanced. This volume has to be conceived of as essentially a volume in water and as at a more or less fixed and rather low temperature. This is the essential physicochemical setting for the problem of the origin of life. It raises further problems: first, the problem of where the external sources of free energy to start the system and to keep it going came from; secondly, of how these energy interchanges within the system were facilitated, as they are in existing life by enzymes; thirdly, of how the system held together and avoided being dispersed in very diluted solution into an extensive ocean; and fourthly, but this comes much later, of how these systems acquired a specific characterization corresponding to a reproduction of certain forms and not of others.

I shall try to deal with the first three of these questions, but shall only indicate some possible solutions to the last. When we have to consider the formation of anything as complicated as life we do not have to conceive of the ways of building the very elaborate molecules that we find at present in living systems, straight up from the atoms. It appears in biochemistry and, indeed, in organic chemistry generally, that the process of synthesis of very complicated molecules proceeds by stages. The first stage is to take atoms and bring them together to form a monomer molecule; the second is to bring these monomers together to form various polymers. The polymers can then be associated in larger groups and finally lead to visible complexes like tissues, fibers, membranes, and muscles. There are, roughly, only about six of these stages between simple atoms and something that you can see in the microscope. Some of these are illustrated in Figs. 1 and 2. This box within box system may be considered as an extension of Charlier's principle which dealt with the universe composed successively of systems of galaxies, galaxies, star groups, stars, and planets. Here we stretch it down through the organic world to the individual atoms. This enormously reduces the amount of complexity that has to be postulated and therefore increases the probability of a structure being made. The associations at each level occur by means of chemical and physical forces of different strengths and range but this is not the place to discuss it. I have dealt with it at length in other papers (Bernal, 1958a,b).

The first stage we have to consider is the formation from the simple molecules that I have indicated, carbon dioxide, ammonia,

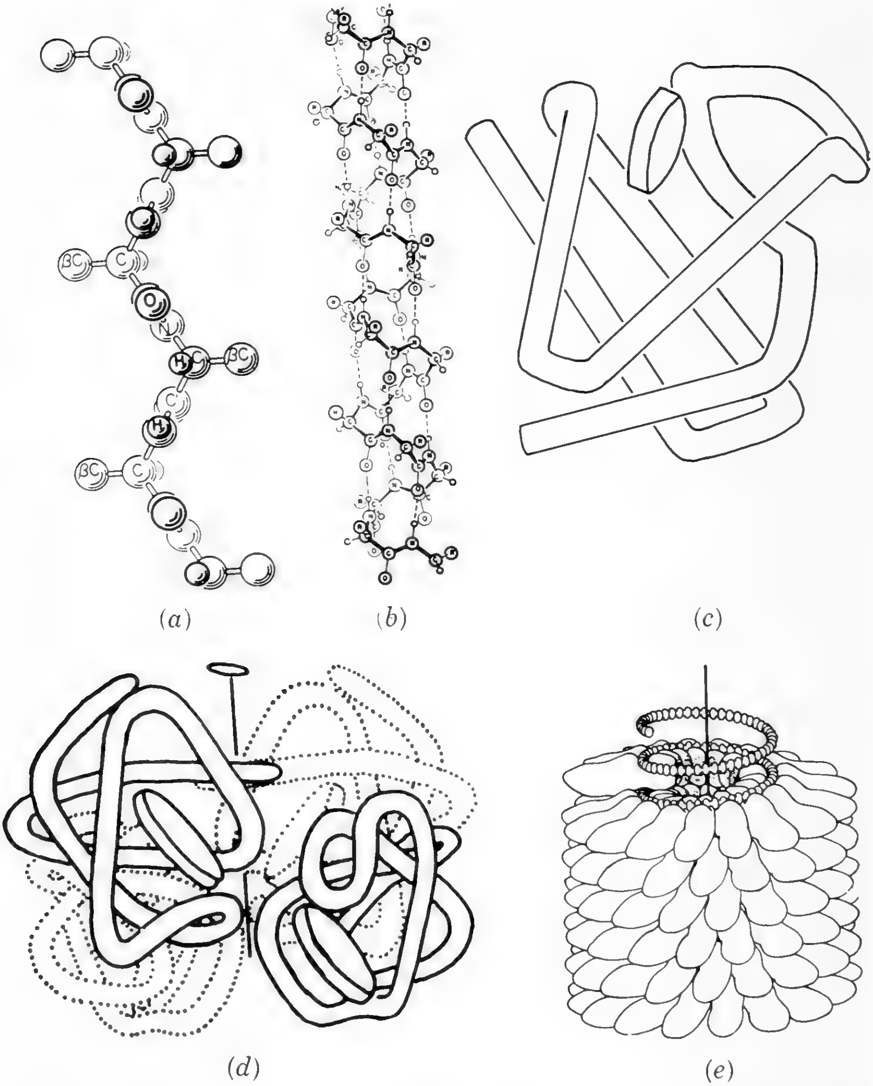

Fig. 1. Hierarchy of polymer complexes: (*a*) primary structure, no intrachain links, polypeptide in β form; (*b*) secondary structure—coiling with intrachain hydrogen bonds, polypeptide in α helix form; (*c*) tertiary structure, folded coils, methemoglobin molecule (after Kendrew); (*d*) quaternary structure (homogeneous type), linked groups of tertiary molecules, hemoglobin structure (after Perutz); (*e*) quaternary structure (heterogeneous type)—linking of different types of ternary protein and primary ribonucleic acid, tobacco mosaic virus (after Franklin).

nitrogen, water, of fairly simple products such as those of the amino acids, vegetable acids, possibly some hydrocarbons, and carbohydrates. This problem has ceased to be an absolute block to further advance since the classical experiments of Miller, inspired by Urey. We now know, as this experiment has been repeated with variations in many parts of the world, that from almost any mixture of simple gases containing the elements hydrogen, carbon, nitrogen, and oxygen and exposed to the kind of exciting agents which are in plentiful supply on the surface of the earth—sunlight, particularly ultraviolet not cut off by ozone, lightning discharges, alpha, beta, gamma radiations from the radioactive materials—will produce a mixture of these simple molecular organic molecules. The proportion depends roughly on the proportion of the original constituents, the more nitrogen, that is, the more ammonia there is in the original constituents, the larger number of amino acids, the less ammonia, the larger the number of ordinary vegetable acids. Obviously, starting with a system of low-energy state, that is, containing CO_2, it will be necessary to feed more free energy into it from the radiation than if starting from a high-energy state involving methane. But the end products are the same, and one of these days we shall understand the process itself because, admittedly, now the experiment shows only that the thing can be done, it has not shown in any detail the processes by which it has been done. Unraveling it is likely to be quite a complicated piece of physicochemical analysis.

Now we may consider the first stage to end with the production of a number of molecules which will be more or less reduced, that is, they will be carbohydrate or amino acids or hydrocarbons, but in all cases they will be soluble in bulk in water, and this raises an enormous problem at the second stage. Because as all such products must come from the primitive atmosphere, which in bulk can only have been a small fraction of the oceanic water, the concentration there can never have been very large. The problem is how can such molecules dispersed in sea water in concentrations of a few parts per million come together sufficiently to produce a further development? Now this process of the further concentration has not been given, I think, sufficient consideration and I, myself, have

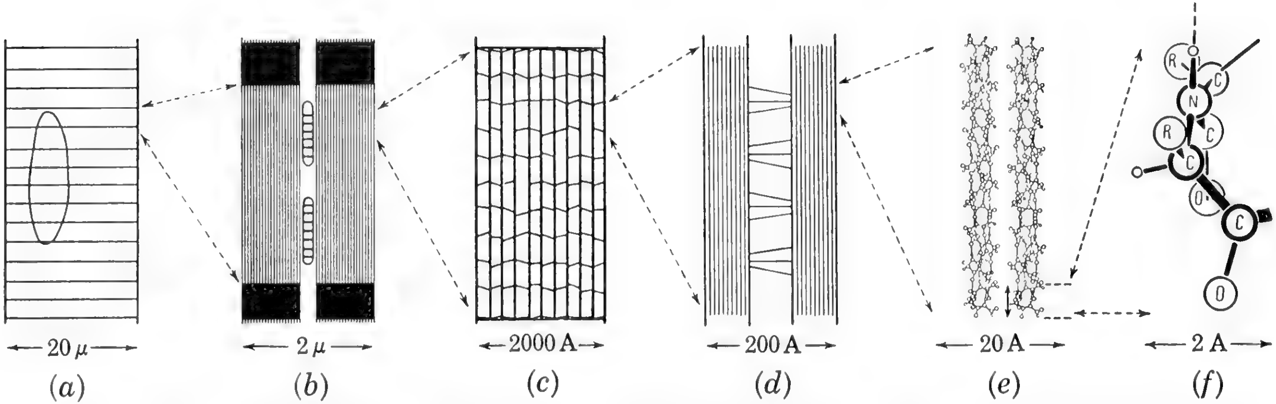

Fig. 2. Six successive orders of a magnification of a muscle cell: (*a*) part of a cell of striated muscle as seen in the light microscope: magnification xy; (*b*) muscle fibril showing one striation Z band and mitochondria as seen in the electron microscope: magnification ×10y; (*c*) part of a muscle fibril showing myofibrils and connecting crosspieces as seen in the electron microscope: magnification ×100y; (*d*) myofibrils showing protein molecular chains, inferred from electron microscope and x-ray analysis: magnification ×1000y; (*e*) chains of myosin (Pauling helix model) as inferred by x-rays: magnification 10,000y; (*f*) part of a polypeptide chain showing two amino acid residues as inferred by x-ray and chemical analysis: magnification 100,000y.

only recently come to see the importance of providing for its very early stages. The essential feature is to move from concentrations of one part per million, let us say, to concentrations of between 1 and 10%. The most obvious way of doing this would be just to take the sea water and boil it down or evaporate it in sunlight, and this has been often postulated: it might be called the rockpool origin of life which was favored by Darwin himself. I have never been happy about this because it is difficult to see what happens after the rockpool has dried out, for although it may be filled again by another tide, anything formed in it will be washed out again and dispersed in the ocean. Consequently, it did not seem to be a very plausible mechanism, but I had not until quite recently come across a better one. Now another and more promising explanation can be derived from the very ingenious investigations of Wilson (1959a,b). He, while studying the composition of snow in the New Zealand mountains, noticed that it contained two features that seemed to him unusual, namely a large content of organic nitrogen and a much larger ratio of potassium to sodium than occurs in most sea waters. This he attributed, by a number of ingenious experiments, to the origin of the snow or the rain in sea mist. This has been known as far as the salt is concerned for a very long time, for it is admitted that most of the salt lakes near the sea and even the sulfur lakes there are produced by the carrying over of dried-out sea mist containing chlorides and sulfates. The most interesting and new deduction, however, of Wilson is that, because the composition of this mist is not the same as that of sea water in bulk, particularly with regard to its content of organic material and potassium, he concluded that he was studying, not a sample of the sea in bulk, but a sample of the surface of the sea. He checked this by an analysis of sea foam, where he found correspondingly large amounts of these constituents. In respect to sea foam it was fairly evident that here were collected a large number of microorganisms, largely dead organisms, but also living bacteria from the surface of the sea. This investigation had a practical bearing in explaining the natural manuring, with nitrogen and potash, of land near the sea. This process occurring today must have occurred from the very beginning.

Even the early seas must have had a surface which was different from their bulk. Any substances which were surface active, such as hydrocarbons and their derivative acids and amines, would accumulate on the surface of the primary ocean and the concentration there may be a hundred or a thousand times as great as in the bulk. Normally this very thin surface layer is not studied—it escapes the nets of the plankton fishers. However, from general physicochemical knowledge, one can predict how it will behave. The surface active materials will be concentrated in the bubbles produced by the breaking waves—in the manes of white horses—and most of it will end up either as mist in the air or as foam or sludge on the beach. Here we have a second process of concentration because with an onshore wind the surface of the sea of hundreds or thousands of square miles of extent can be deposited along a few miles of beach. How effective such a process is appears only too unpleasantly on all our tar-covered beaches on which practically all the oil effluent of ships is now concentrated.

The surface active molecules would have appeared in the earliest times as a thin layer of sludge left on the sand or mud by each receding tide. It is here we might expect to find the hydrocarbon molecules postulated by both Urey and Oparin. These may, indeed, have entered the sea as Oparin first proposed, from fissures leading deep into the earth. This new hypothesis of the superficial formation and onshore drifting of the original materials from which life was formed removes one of the greatest obstacles to the plausibility of an inorganic origin of life in the ocean. In a classical analogy, life no longer comes straight from Poseidon but, like Aphrodite, it was born of the sea foam. Less poetically but more accurately, it may be likened to the wind skimming the scum of the oceanic cooking pot and depositing it on the beaches.

The fate of the material deposited from the sea surface would differ very much according to the kind of coast onto which it is driven. Clearly a rocky coast would not lead to any fixation at all, and a sand coast not very much more; where fixation would certainly occur is in a mud, particularly an estuarine mud. Today the composition of estuarine muds as deposited layer by layer by every stand of the tide is predominantly formed from the remains of organisms. In the earliest times it must have been the organic molecules which preceded life that were so deposited. There they would have been strongly absorbed by the clays. This is the hypothesis I put forward some thirteen years ago, and I think now it can claim a certain amount of support from experiment. By such a mechanism of deposition and absorption it is possible to build up quite a considerable amount of organic material layer by layer as each deposit is put on top of the other. Every thick clay bed today contains its appropriate amount of organic material, in some cases very large amounts; there are marine clays which contain as much as 2% of oil and this, indeed, may be the source of most of the oils which are exploited commercially.

This organic trapped material, however, does not usually remain indefinitely in the clay of an active estuary; in most cases the clay is in turn eroded by the runoff streams, and the mud is returned to the general circulation of suspended mud. This will not be the same as the original organic material for, while absorbed on clay, it may have undergone chemical changes. This process of deposition and erosion is repeated indefinitely and the whole material, organic and clay together, is worked over and over again. As it lies on the wet surfaces at low tides it is, of course, exposed to sunlight, heated quite considerably, and liable to chemical changes. Now one of the chemical changes which is the most interesting and which has been checked by the work of Akabori (1959) has been that of polymerization. He has actually carried out the experiment of polymerizing the simplest amino acid, glycine, on a clay base with ultraviolet light and finds it produces polyglycine. Such polymerizations, but naturally much more complicated, must have occurred on the early mud flats. The problem is to see not so much how the polymer is formed but how it is removed from the clay, and this still requires to be demonstrated. We may by a negative argument postulate that this separation did take place because polymerized colloidal substances are found in all organized bodies, and on the other hand clay is not found in them. They must at some point have separated themselves from the clay.

Here my ideas rejoin those of the original Oparin hypothesis that the polymerized materials, particularly if they are heterogeneous in character, will tend to form the little coacervate drops on which he bases the latter part of his theory of evolution of life. The essence of such coacervates is that they can retain their individuality and float around in water without dissolving; in other words, once polymerization occurs, there is no more danger of destruction of life by dilution. But this is not all. Here again I have been led to modify somewhat the general ideas of Oparin and many others who have discussed the origin of life. One way of considering the origin of life is to consider that there was a definitely preorganic stage in which very large amounts of materials were synthesized by purely inorganic means and then gathered together and perhaps associated in coacervates, after which metabolism started. I do not take this view now. I believe that metabolism in the wider sense was occurring all the time, and the present day metabolism is simply a refinement of the earliest quasi-inorganic metabolisms. In other words, I believe that the method of living evolved at the same time as its material.

This would imply that even before the stage of polymerization, that is, still in the adsorption or clay stage, something of the nature of the balanced chemical reactions would have been occurring through the whole extent of the mass—what I have called the *subvital areas*. What would be the character of these changes? We can see something of this by considering present day biochemical changes which may be characterized by two general features, first of all enzyme actions or specific catalyst actions. These enable certain chemical reactions, which would have occurred anyhow, to occur very much faster. Enzyme actions are responsible for every change in present living organisms. But with the enzymes are associated substances called coenzymes that have a different function. Whereas the enzymes are specific, that is each enzyme helps to carry out one particular reaction, the coenzymes are much more generalized, they are much fewer, and their function is to transfer energy from one part of the system to the other, and thus to enable chemical reactions, which otherwise would not take place, to occur by transferring the extra energy provided in other chemical reactions. This is a way of balancing accounts which prevents, as it were, the system from heating at one place or freezing in another. It keeps the wheels turning. Now the enzymes of today are all proteins; the coenzymes of today are nearly all what we call nucleotides, that is, triple complexes of a nitrogen base, usually purines or pyrimidines, a sugar, and phosphoric acid; much too complex a molecule to have existed in the beginning or to have occurred by chance.

Unless it is desired to push back the doctrine of special creation to the creation of enzymes and coenzymes (there is a school that would take one of these, namely the coenzyme in the polymerized form as nucleic acid) as the beginning of life, unless then we are prepared to take such an easy way out, we must assume that before there were enzymes to carry out the catalytic reactions in metabolism there were some other agents that did it, not so well, but sufficiently well for the slow times of the origin of life. Similarly, before there were any coenzymes there must have been some other and less efficient means of transferring energy from place to place. I think we are just beginning to see what these earlier forms of such protoenzymes could be, thanks to the work of Calvin (1959), Nicolaev (1959), and others. For the protoenzyme action it would appear that iron coordination compounds are capable of speeding up many chemical reactions by factors, not of ten thousand but of five to a hundred. Such compounds of iron or of other transition elements, copper and nickel, would form spontaneously from any solution in which there were nitrogenous compounds of the type of amino acids or simple purines, and these may well have been the protoenzymes. For the protocoenzyme we have a clue in the presence of phosphoric acids, particularly of the chain-linked metaphosphoric acids. These have the property, in breaking up and re-forming, of liberating and absorbing energy in the form of the so-called energy-rich phosphate bond. In my view, therefore, the story of metabolism runs absolutely parallel with the story of concentration leading to the formation of subvital areas. In fact, it is only when we reach the coacervate stage that we can talk of organisms. Before that I think we are quite right to talk about life without organisms, an extensive form of life not broken up into small packets.

To interpret the subsequent stages which lead to some kind of definitive organism, it is first necessary to find in what way it is possible to combine in one small unit all the essentials for metabolism. This was not necessary before, because all the essentials would have been found somewhere or other over a large area and sooner or later—they must have taken years to do so—got to where they were wanted. Now the major essential for metabolism, without which the enzymes and the coenzymes could not function, is a source of energy, and this energy can be provided either immediately by light or it can be drawn from substances in which energy has been stored by the previous action of light. These alternatives form the fundamental distinction between the vegetative and the animal way of living, of which the vegetative is clearly the most primitive.

It happens that these iron and other metal coordination compounds that I have mentioned are suitable not only for carrying out enzyme actions but also can absorb light and, being colored, can absorb it where it is very much stronger in the visible region of the solar spectrum. We call it, of course, the visible region, because we have built up chemical receptors that react to the predominant frequencies emitted by the sun. The appearance of photosynthesis is, in my opinion, the key to the development of the organic life as we know it. How complicated a structure need be to have the requirements of photosynthesis and enzymic transformation in one, we cannot say, but it must be relatively small on the vital scale though large on the molecular scale. Kamen (private communication) has found in some of the red bacteria, which are probably very primitive organisms, molecules as small as a virus, that is, about 200 A across, which contain nucleotides, enzymes, and photosynthetic plastids capable of building up sugars from carbon dioxide and water, in other words, all the necessary works of an organism.

Whether such small bodies can ever have existed independently is another question. However, we do find them in present-day life usually as separate components in the so-called organelles or small bodies that exist inside cells, such as the chloroplasts responsible for photosynthesis, the mitochondria that carry out the enzymic changes which constitute the metabolism, the microsomes that synthesize protein and contain ribonucleic acid, and the deoxyribonucleic acid-containing chromosomes. It may well be that all these represent specialized versions of what was originally an all-in living molecule. This is not the type of living molecule that Oparin attacks, I think quite rightly, because this is essentially a complex of molecules having between them all the necessary functions, not the simple, naked nucleic acid molecule which can do nothing by itself. On the other hand, it may very well be that in the general symbiosis of the more primitive mud stage, these elements developed separately and only came together as a kind of enclosed symbiosis containing all the elements out of which cells are made.

To complete the picture, only one further thing is required, namely the development of some means of blocking off the cell. The coacervates of Oparin are unenclosed—small molecules could diffuse in and out of them as well as right through them. In consequence, all chemical processes occurring in them must be done in common; the greatest isolation that can be maintained is due to the gradients of concentration of one chemical or another. However, there is one group of organic molecules, the lipids, with long molecules that pack together in sheets, which are able to supply just those outer and inner partitions which are necessary. I think that the appearance of lipids made possible, first of all, a separation between the original coacervate and its environment, making it effectively a little box or cell, and then the separation of the different parts of this internal structure from each other. One part could become a nucleus containing essentially the memory elements needed for regulation and reproduction, and another part could contain the mitochondria for the metabolic processes, and so forth. The new knowledge of the cell gained by the use of the electron microscope shows it as not just one single city surrounded by a wall, the old cell wall that we have talked about for eighty years or more, but as a whole country including many cities and villages, each with its different capacities and, as it were, trading with each other. This latter evolution, however, falls outside the scope of this paper.

To sum up, what I feel is that we now have the skeleton of a story of the origin of life of which the details need to be filled in and which, I think, can be filled in by a close and active combination of different techniques. True there is not at present, and probably there never will be, any single person who can himself command all these techniques, but this does not make the task an impossible one; rather it is a challenge to collective human ingenuity. The kind of cooperation which we have had at this Congress, makes it possible to envisage some kind of extended cooperation, particularly between the workers in the sciences of earth, sea, and air, with the biochemists and the biophysicists. In the process of filling in the story that I have set down here they may well destroy it but only to remake it in a much more satisfactory form.

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NOTES ADDED IN PROOF

A recent study of the carbonaceous meteorites has, in my opinion, completely altered the picture of the origin of carbon and nitrogen compounds on the surface of the earth. Mason (1960) has shown that these very rare types of meteorite, far from being an aberrant product derived from proto planets, are in fact the nearest we can get here on earth to the primary cosmic dust. The key to this is the demonstrated presence in them of the mineral chlorite, a *hydrated* silicate of formula $(MgFe)_3Si_2O_72H_2O$.

Dr. Mason has shown convincingly, in my opinion, that from these meteorites all the other types—chondrites, containing the anhydrous silicate olivine $(FeMg)_2SiO_4$—can be derived by simply heating to 600° corresponding to the abundant and stable chondritic meteorites. On further heating, the carbonaceous material reduces the iron-rich olivine to metallic iron in small particles in the stony iron meteorites. If such meteorites agglomerate into bodies of planetary size of 100-km diameter or if overgravitational segregation occurs, the iron sinks to the center while the olivine is melted and recrystallized and carries with it other light elements such as calcium and aluminum, which crystallize as anorthite, $CaAl_2(SiO_4)_2$.

It is from the breaking up of such bodies that Mason suggests that the achondrite and iron meteorites are derived. This revolutionary theory of meteorite formation is not yet generally accepted but, whether true or not, there can be no doubt that carbonaceous meteorites exist at the present time and may have been much more abundant in the past. This means that we may have here an important, perhaps the major, source of the carbon compounds on which life was built.

A study by Müller (1953) on the nature of the carbonaceous fraction of the meteorites extractable by organic solvents shows that they are very complex and contain fractions of a bituminous character—but different from terrestrial bitumen—which volatilizes at temperatures between 100° and 300°C. This bitumen also contained nitrogen, sulfur, and chlorine, the last in an organic form. It would seem to take the form of a complex of an aromatic polyacid, like humic acid, and iron.

On the basis of these data it is possible to build a self-consistent picture of the building up of planets from an original finely dispersed meteoric dust formed at low temperatures. The composition of the mineral chlorite corresponds to the cosmic abundance of the atoms of magnesium, silicon, and iron. Even more important for the later developments is the presence of water in a form not removable under 450°C. Minute paramagnetic flakes of chlorite a few hundred angstroms in diameter and 15 angstroms thick, magnetically oriented, may well be responsible for the polarization of stellar light. In the outer zones of the solar system, such flakes could serve as nuclei for a deposit of solid methane and ammonia known to exist from Jupiter outwards. Now through the action of cosmic rays or solar protons on this finely dispersed matter, it seems likely that a certain degree of polymerization takes place to form a bituminous layer surrounding the chlorite core. Some of these bitumen-coated meteoritic flakes may then agglomerate into snowball-like aggregates which would have a density of about $0.1 \rightarrow 0.3$. These in turn would weld into larger bodies until, with a radius of some hundreds of kilometers, the center would be crushed and highly heated by gravitational forces. This would result primarily in the expulsion of volatile hydrocarbons and the conversion of chlorite to olivine chondrites. Further heating in the central part of such a body would give rise to a chemical reaction between the residue of the bitumen and the iron-rich olivine, resulting in the production of metallic iron which would separate by gravity and leave an iron-poor silicate slag, such as is observed in the iron meteorites and achondrite stony meteorites. At a certain stage of agglomeration, when a diameter of about 8000 km or slightly smaller than Mars and larger than the moon is reached, water can no longer escape from the system. Only then is it possible for oceans to form and the whole complex of weathering-deposition, mountain building, and continent moving can be set in motion.

This new evidence has a most important bearing on the question of the origin of life. It sets the first purely chemical stages further back to at least 4000 million years. Indeed it can be said that in the making of the first carbon and nitrogen compounds the origin of life is much earlier than that of the earth.

It also makes the problem of the primitive accumulation of both organic substance and free energy much simpler. Instead of having to postulate, as Oparin did, that this accumulation was produced by solar radiation in the relatively thin layer on the surface of the primitive earth, it can be spread over a hundred million times greater area of cosmic dust.

Only some of this primitive accumulation would be retained in a formation of a planet of the size of the earth, for only the outer layers would be free from the heat-induced chemical processes which effectively would convert carbon to iron. Qualitatively, it would mean the presence not so much of gaseous hydrocarbons in the atmosphere, as of liquid and solid complex carbon and nitrogen compounds floating as a film on the surface of the primitive oceans. The quantity might be quite considerable. Analysis of a whole carbonaceous meteorite shows the presence of 2% of carbon and 0.3% of nitrogen. It would, however, take a long time for such quantities to be liberated even from the upper layers of the crust. Consequently, the operation of the shoreline concentration process described in the 1958 paper would probably still be required.

The net result of this new approach is to a large extent to support the original Oparin hypothesis, with the difference that his initial gaseous hydrocarbons and ammonia would be replaced by solid or liquid energy-rich carbonaceous and nitrogenous compounds, and most apt to develop further into those on which life would be ultimately based.

Further, it would dispose completely of the criticism put forward by Hull (1960) that photosynthetic degradation must accompany photosynthetic creation of complex compounds from simple molecules. I have already pointed out (Bernal, 1960) that the removal of the reaction products would also help to preserve them, but Mason's hypothesis would very much strengthen my argument.

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Origin of Life in the Oceans

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ALL attempts to prove spontaneous generation of life directly from inorganic matter either under natural or laboratory conditions have been in vain. It is more and more evident that the origin of life on the earth could have taken place only as an integral part in the overall development of our planet. Available data show that the origin of life represents a long-term, one-sided process toward increasingly complex organic substances and of complex open systems synthesized from these.

We certainly cannot reproduce the whole process of the origin of life, which took place over a period of billions of years, in the same form as it took place in nature. We can study only isolated steps in this process either under natural conditions when they have remained as they were at the time the earth was devoid of life or under artificial conditions reproduced in our laboratories.

On the basis of all our knowledge, three chief stages essential to the origin of life may be outlined provisionally. The first is the primary (abiogenetical) formation of the simplest organic substances, hydrocarbons and their closest oxygen, nitrogen, sulfur and phosphorus derivatives. The second is the conversion of these substances, basic for the synthesis of the most complex organic compounds characteristic of life, proteins, nucleic acids, porphyrins, lipids, etc. Finally, the third stage is the formation of multimolecular complexes, open systems, from the latter compounds. Subsequently, they are converted into primitive living organisms.

The development of the first of these stages is closely associated with the planetary cosmogony itself. The emergence of the simplest organic substances must have taken place during the formation of the earth and in the early stages of its development.

Astronomical studies of the surface of the stars, interstellar gaseous dust, atmospheres of other planets, meteorites, and comets prove the necessity for the formation of the first hydrocarbons during the formative stages of our planet and its subsequent evolution. The question is merely which of many possible ways was this accomplished.

It is now generally accepted in astronomy that the earth, as well as the other planets of the solar system, arose from gigantic nebulae of gas and dust which once surrounded the sun. Study of the chemical composition of this gaseous dust shows the presence of methane and perhaps more complex hydrocarbons. However, with careful physicochemical analyses of phenomena occurring during the formation of planets, Urey showed that when the clouds of gas and dust particles became aggregated into protoplanets and planets, a considerable amount of methane and other volatile gases must have disappeared from the vicinity of the earth to the region of large planets where they may be found today. According to Urey, graphite and carbides were the chief forms of carbon in the emergent earth. From these, hydrocarbons must have been synthesized abiogenetically during the formation of the earth's crust, particularly at the time when carbides could react with hydrated rocks in the deeper layers of the earth's crust. However, although the formation of the earth's crust began early in the development of our planet, it cannot be considered complete even now. Hence, even today we may expect to find processes for the formation of simple hydrocarbons in the deeper layers of the lithosphere, where reducing conditions prevail and where all traces of life are lacking.

Many geological observations seem to justify this supposition. The processes for the abiogenetic synthesis of hydrocarbons is now taking place, although on a very limited scale. Hydrocarbons in the basement rocks are isolated from living organisms or any products of their decomposition. Here, in granite fissures, such gases as methane, ethane, propane, and small amounts of liquid hydrocarbons occur. These could have arisen only abiogenetically.

Because these hydrocarbon deposits are usually of no commercial value, geologists have given them little attention. Nevertheless, their occurrence makes it possible to study the first stages in the origin of life under natural conditions. The original hydrocarbons formed in the earth's crust were only the first step in a long series during abiogenetic organic evolution which took place when the earth was still devoid of life. This took place over a period of many billions of years and led to the emergence of very complicated organic substances with large molecules similar to those in living matter.

How can we recognize the processes in the chemical evolution for the second stage which took place billions of years ago when the earth was uninhabited by living organisms? At first sight, it appears that methods of geochemistry could be used to study the abiogenetic conversions of carbon compounds taking place today under natural conditions on the earth other than in living matter. These should give the simplest and most reliable answers to the problem. Such a study can certainly give us many valuable data, but it must be remembered that life, having once originated on the earth, radically changed many conditions on the surface of our planet. At present, many of the phenomena which took place in the past do not now occur, but new processes have arisen which did not exist on the surface of the lifeless earth. Therefore, we cannot compare contemporary geochemical data directly with that for the early epochs of our planet. To study the conversions of organic substances, however, we must simulate these early data in laboratory experiments, which artificially reproduce conditions on the primitive earth. Indeed, only a small portion of the hydrocarbons synthesized under abiogenetic conditions could remain in the lithosphere. All volatile carbon compounds gradually escaped from the earth's crust into the atmosphere in the past, and this also occurs now in the case of the natural hydrocarbon gases.

The atmosphere of the lifeless earth differed from the present atmosphere principally in its reducing character. This is suggested not only by general theoretical considerations, but also by many direct geological observations. Most of the free oxygen of the present atmosphere was undoubtedly formed by the activity of green plants. If the earth again became devoid of life, free oxygen would very soon disappear from its atmosphere due to adsorption by rocks. Hydrocarbons released into the atmosphere could not be directly oxidized by gaseous oxygen, but could react with water vapor, ammonia, hydrogen sulfide, and other gases in a reducing atmosphere. Short-wave ultraviolet light in the absence of an ozone screen would penetrate the atmosphere and contribute to this interaction. Another significant energy source for organic syntheses might be static electric charges in the atmosphere. In recent years, conditions which could have taken place in the primeval atmosphere of the earth have been reproduced under laboratory conditions. Even such a relatively inert gas as methane can serve as the basic substance in the synthesis of various organic compounds, as shown by S. Miller's experiments. He obtained amino acids, the important precursors of protein molecules by using charges of static electricity in the presence of methane, hydrogen, ammonia, and water vapors. Similar syntheses of amino acids were carried out by T. Pavlovskaya and A. Passynski using ultraviolet light. Many others have suggested the possibility that amino acids, precursors of the porphyrins, etc., could be formed under such conditions.

As they gradually became more complicated, organic substances were no longer gaseous. Hence, they became increasingly concentrated in the primary hydrosphere of the earth rather than in the atmosphere. Thus, most organic compounds must have accumulated there. Here, then, large molecular substances were principally formed and changed into multimolecular systems, from which life emerged.

Unfortunately, the waters of modern seas and oceans do not provide an environment favorable for reproducing these processes under natural conditions. First, these waters as well as the atmosphere are very rich in free oxygen. From investigations aboard the Soviet research ship *Vitiaz*, it appears that even the waters of the greatest ocean deeps are saturated with oxygen for the most part. Only in some unusual cases, such as in certain Norwegian fjords, are reducing conditions found. Even here, as everywhere else, the waters are well populated, particularly with microbial organisms. In the presence of these, however, it is very difficult to distinguish abiogenetic processes which could have developed in the primary hydrosphere from biogenetic ones which only occur today.

Thus organisms vitiate our results: they excrete into the external inorganic medium, in quantity, substances resulting from metabolism. They also absorb and ingest other substances in their anabolic processes. Thus, they radically alter the course of the chemical reactions in their environment. Therefore, we must learn about the conversion of organic substances in the waters of the earth's hydrosphere, chiefly through a comparison with the phenomena observed under experimental conditions. A great many investigations have shown how through a gradual polymerization and condensation of organic substances protein-like substances, such as polynucleotides, porphyrins and other complex organic compounds abiogenetically in the waters of the primeval ocean. I will only mention here the papers of Sh. Acabori, M. Grunberg-Manago, and others published in the *Proceedings of the Moscow Symposium on the Origin of Life.*

Until recently, the viewpoint was widely held that life first arose on the earth in the form of a single "living" molecule. This supposed that a very complex molecule (i.e., a molecule of nucleoprotein or nucleic acid) was somehow formed in the waters of the primeval ocean. The inner structure of this molecule determined the vital properties and in particular the ability of this first "living molecule" to reproduce and propagate itself. This theory of the origin of life was chiefly connected with Morgan's work on the nature of the gene and with work on viruses. However, modern biochemical knowledge ruled out the possibility that vital processes can develop from a single molecule. Thus, the ability of a virus nucleoprotein to reproduce is only possible because of its interaction with the multimolecular complex of the protoplasm of say the tobacco plant or of some other host. Those laws of thermodynamics and chemical kinetics, which alone determined the course of the processes in the waters of the primeval ocean, may explain the emergence of only polypeptide or polynucleotide polymers in general and not that of compounds with some established "life-determining" structure. Therefore the emergence of such a structure is usually considered the result of a "happy accident" with a very small probability. This certainly rules out the possibility of any experimental approach to this problem together with its rational solution.

Much more promising is the idea of open multimolecular systems or coacervate drops which were the original precursors of primitive organisms. The formation of coacervate drops is the most vigorous means for the concentration of large molecular compounds from dilute solutions. At the same time, the fact that protoplasm, the contemporary carrier of life, has the structure of a complex coacervate must also be recognized as a very important one.

Modern laboratory investigations of coacervate drops permit us to outline (certainly only hypothetically) both the process for their formation and the course of their further evolution in the waters of the primeval ocean. At the beginning, on the emergence of coacervate drops, two circumstances existed which were very important for their subsequent evolution. On the one hand, certain individual physicochemical peculiarities within each drop affected the processes within that drop. On the other, any chemical processes occurring within the drop and, in particular, any combination of them must affect the future of that drop. Some contributed to greater dynamic stability of the drop, but others were unstable and led to the disappearance of a given coacervate system. This may be observed in our experiments on introducing various catalysts, particularly enzymes, into coacervate drops. Thus even at this early stage in the coacervate drop evolution, there appears to have been a certain "selection" in the basic colloid systems as a result of their suitability for preserving the particular system under the conditions of its continuous interaction with the surrounding medium.

With the mass growth of the basic coacervate systems in waters of the primeval hydrosphere resulting from this "selection," only those could exist and develop within which the reactions of disintegration and synthesis were so coordinated that recurrent chains and cycles of reactions were stable. Consequently, the formation of new substances or structures can occur again and again. With stability caused by the recurrence of interconnected and coordinated reactions there arose the capacity for self-reproduction, one of the characteristics of living organisms.

From this point on one may speak of the emergence of life. At this stage in the evolution of matter, natural selection acquired its biological sense in full measure. Under this check on the evolution of organisms, metabolism, a characteristic of living matter, then became more complicated and was improved. Through natural selection, intermediate systems with imperfectly organized metabolism disappeared from the earth. A comparative study of the metabolism in the most primitive organisms still in existence make it possible to judge the way in which the newer extremely efficient order of chemical reactions so characteristic of the more recently developed higher animals and plants gradually evolved.

From studies in comparative biochemistry, it clearly appears that some metabolic systems arose early and are typical of all organisms without any exceptions. Others, on the contrary, developed much later as additions to structures already in existence. The capacity for organic, heterotrophic nutrition or the utilization of ready-made organic substances as building materials together with an energy source is the most primitive form of metabolic organization. It is innate in the structure of living matter and inherent in all living organisms without exception. The first organisms were doubtless heterotrophs. Such studies also show convincingly that these were in addition anaerobes, as it is an anaerobic metabolism which provides energy for all organisms. This is quite understandable in view of the fact that both the primeval atmosphere and hydrosphere had reducing characteristics.

In the development of life, the supply of abiogenetically formed organic substances on the earth's surface gradually became exhausted, because the development of life proceeded more rapidly than did the formation of these substances. This change in the conditions for existence increased the importance of those organisms which on account of their ability to absorb light could synthesize organic substances from inorganic carbon compounds or from carbon dioxide in the atmosphere. In this way photosynthesis, a new biological method for the formation of organic substances, replaced the earlier inefficient and slow abiogenetic formation of such substances. This occurred because photosynthesis came to dominate and monopolize the metabolic process, a situation which has been efficient until the present day.

The emergence of photosynthesis altered all life on the earth.

It created an abundance of organic substances and at the same time led to the appearance of free gaseous oxygen. This had hitherto been lacking on the earth's surface. It changed the character of the chemical processes and enabled most living organisms to change the energy source used in metabolism, to develop new systems for oxygen respiration, and thus to utilize completely the energy to be derived from organic substances.

With the appearance of photosynthesis, the evolution of both plants and animals proceeded at an ever increasing rate as shown by paleontological data. If we now try to view the whole history of evolution, at a glance, from the moment our planet was formed until the present, we shall see that with each new step in its development the rate of development increased rapidly. The general development proceeds with time as if on an exponential curve turning steeply upward (Fig. 1). During most of its existence our planet was devoid of life. The abiogenetic evolution of organic substances took some billions of years. With the origin of life, the development proceeded much more rapidly. The drastic biological changes took only some hundreds or even scores of millions of years. The formation and biological development of man took only a million years. Finally, social changes occurred in the course

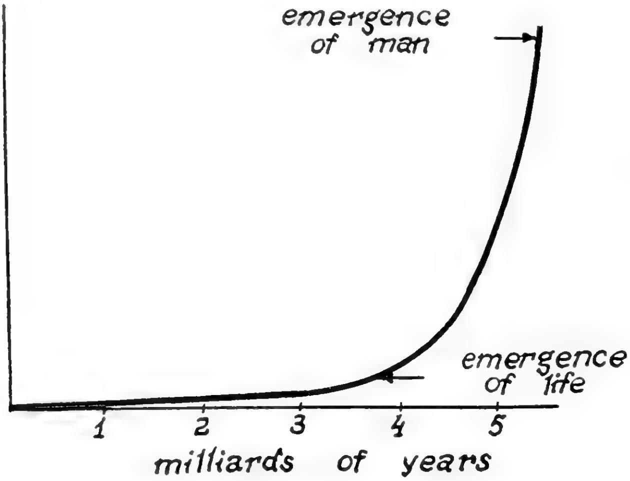

Fig. 1

of a thousand years or perhaps only of a few centuries. Now we notice obvious shifts in the development of human society within only a few decades. With new forms of organization, old ones were actually retained, but their importance for further progress became insignificantly small. The older forms develop considerably more slowly than do the new ones. With the origin of life, the slow, abiogenetic synthesis of organic substances lost its significance in evolution, as it could not compete with the new, highly organized more rapid processes of metabolism. It is this situation which rules out any possibility of spontaneous generation today. The emergence of new organisms is now only possible by the new, extremely efficient method for the synthesis of living material from other living matter.

It may sound paradoxical, but life does not rise *de novo* just because it has once done so. Let us imagine a tank of water without any living organisms in it but with various organic substances dissolved in the water. If left alone for a considerable time, the synthetic processes outlined above would occur but slowly. Perhaps after many millions or even billions of years this might lead to the origin of life. But if we were to introduce into our tank, organisms already in existence (i.e., bacteria), the course of events would be quite different. In that case the more highly developed biological form of organization would come to the fore and dominate. Then the transformation of inert materials to living matter would not follow the slower processes, but rather would proceed in the new way through the metabolic conversion of organic substances in the solution into living protoplasm with tremendous rapidity. Therefore the primitive (abiogenetic) origin of life would simply not have time to take place and thus it would not occur at all.

Certainly, if as a result of some catastrophe as a consequence of the atomic madness of mankind, life were to disappear on the earth, the curve presented in Fig. 1 would fall sharply to its base. Then it might be expected to turn upward once more, although in perhaps a somewhat different way. Let us hope, however, that this will not happen and that the curve of progress of mankind will continue to rise.

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Geological Record on the Ocean Floor*

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GEOLOGICAL events with worldwide or large-regional effects such as climatic change, volcanic activity, evolution of the ocean, and interaction with outer space are often recorded on the deep ocean floor far away from the continents, in a manner that makes this record advantageous for quantitative interpretations. The Pacific basin (Fig. 1) has some characteristics that make it particularly well suited as a recipient of representative sedimentary sequences.

The marginal trenches and ridges effectively bar turbidity currents from the central basins; the lack of such protection in exceptional cases such as along the coast of the northern United States and Canada has resulted in widespread detrital deposits over adjacent areas of the deep ocean floor. On account of the approximately isometric shape and the large dimensions of the Pacific Ocean, several of its topographically protected basins are separated by several thousand kilometers from the continental sources of windborne detritus, and the eolian component of the sediment thus is largely attenuated.

Another important feature of the Pacific Ocean is that its vast open area extends into high latitudes both in the Northern and the Southern Hemispheres. This makes it possible for the wind-driven circulation to develop without interference from land masses in a far more pronounced way than in the Atlantic and Indian oceans. At the equator, the forces arising from the rotation of the earth, cause cold, deep water, rich in nutrients, to ascend to the surface where the sunlight makes photosynthesis possible (Fig. 2, middle graph). The resulting zone of highly increased organic productivity

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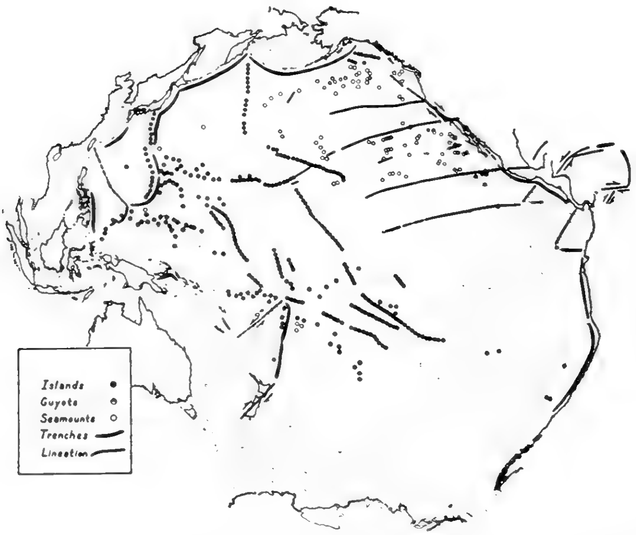


Fig. 1. Structural features of the Pacific Ocean (Menard and Fisher, 1958).

marks the position of the geographic equator on the surface of the sea, and the rain of organic remains which fall down on the ocean floor below makes a permanent record of the position of the equator at any given time.

The nature of this record is indicated in the lower graph of Fig. 2, a generalized meridional cross section through the top 5-m layer of the sediments, at about 125° W Long. Owing to the strongly increased production of calcareous and siliceous plankton, responsible for the bulk of the biogenous contribution to the sediment, the sedimentary strata attain a maximum thickness below the equator. It is obvious that we here have a means for determining its position in the past, inasmuch as any displacement of the geographic equator should be traceable as a corresponding displacement of the thickness maximum of the strata. Provided the position of the equator is determined in two places, preferably about ninety degrees apart, the position of the poles is also fully determined. Other parameters, which are still more useful for this purpose because of their larger gradients toward the equator, are the rates of accumulation of fossils, minerals, or chemical elements

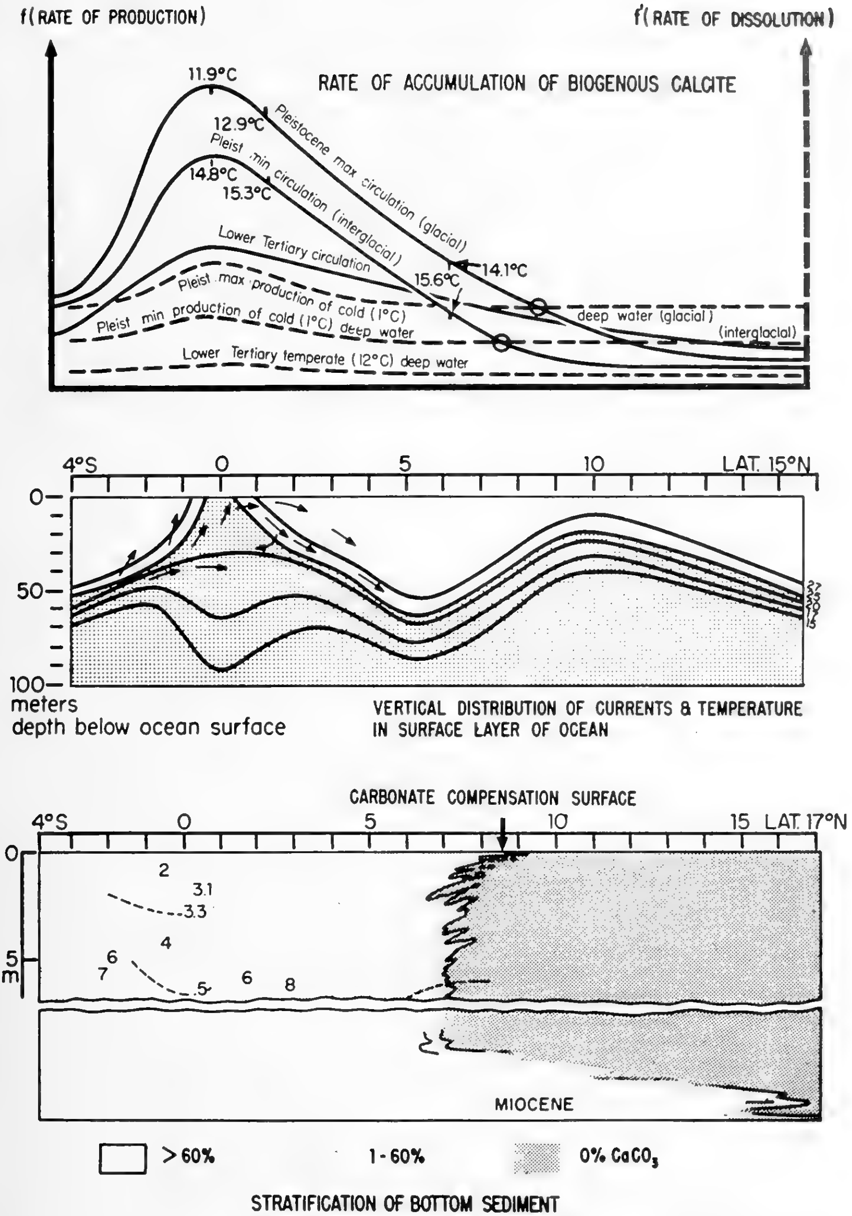


Fig. 2. Meridional profile at approximately 130°W Long showing the distribution of temperature and vertical motion in the surface layer of the ocean (middle graph), the stratification of the bottom sediment (lower graph), and the interpretation of the sedimentary record in terms of paleotemperature and rates of production and dissolution of calcium carbonate from planktonic organisms (upper graph) (Arrhenius, 1959a).

which are concentrated by the biological processes at the equator and which do not to the same extent as the major biogenous sedimentary component, calcite, suffer from dissolution (Fig. 2, top graph). These rates can be expressed in relative units as mass of the biologically concentrated component per unit mass of inorganic deposit. As a convenient measure of the latter have been employed elements like aluminum or titanium in such remote and protected basins where evidence for a reasonably low variability in the contribution of inorganic components has been obtained. In Fig. 3 are plotted the results by Goldberg on the rate of accumulation of barium in the Postglacial stratum in the east Pacific as a function of latitude, showing a sharp maximum under the equator with about twenty-five times the rate prevailing at higher latitudes, and a drop to $1/e$ of the maximum value at a distance of about $1\frac{1}{2}$ degrees north and south of the equator. The rare earth elements and zirconium are still more promising than barium in this respect, as they are laid down in the form of highly insoluble phosphates which do not appear to migrate in the sediment.

In the sedimentary sequence available at the equator by present coring methods we do not reach further back in time than to the Middle Pleistocene, or roughly half a million years. During this time, the pole has remained constant within the resolution of the present sampling grid which is about four degrees of latitude. A 500-m long core in the equatorial sediment bulge would probably take us back at least into Middle Cretaceous strata, and to a time

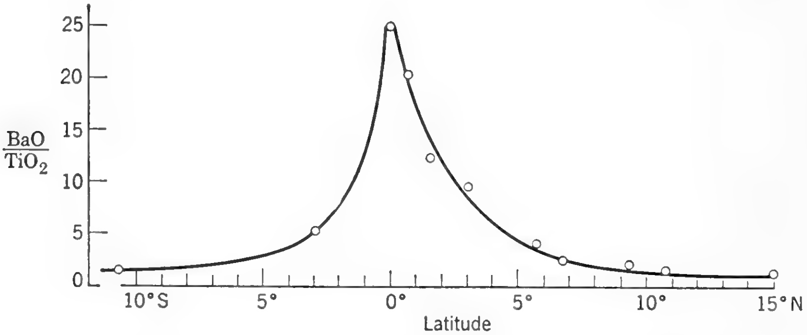
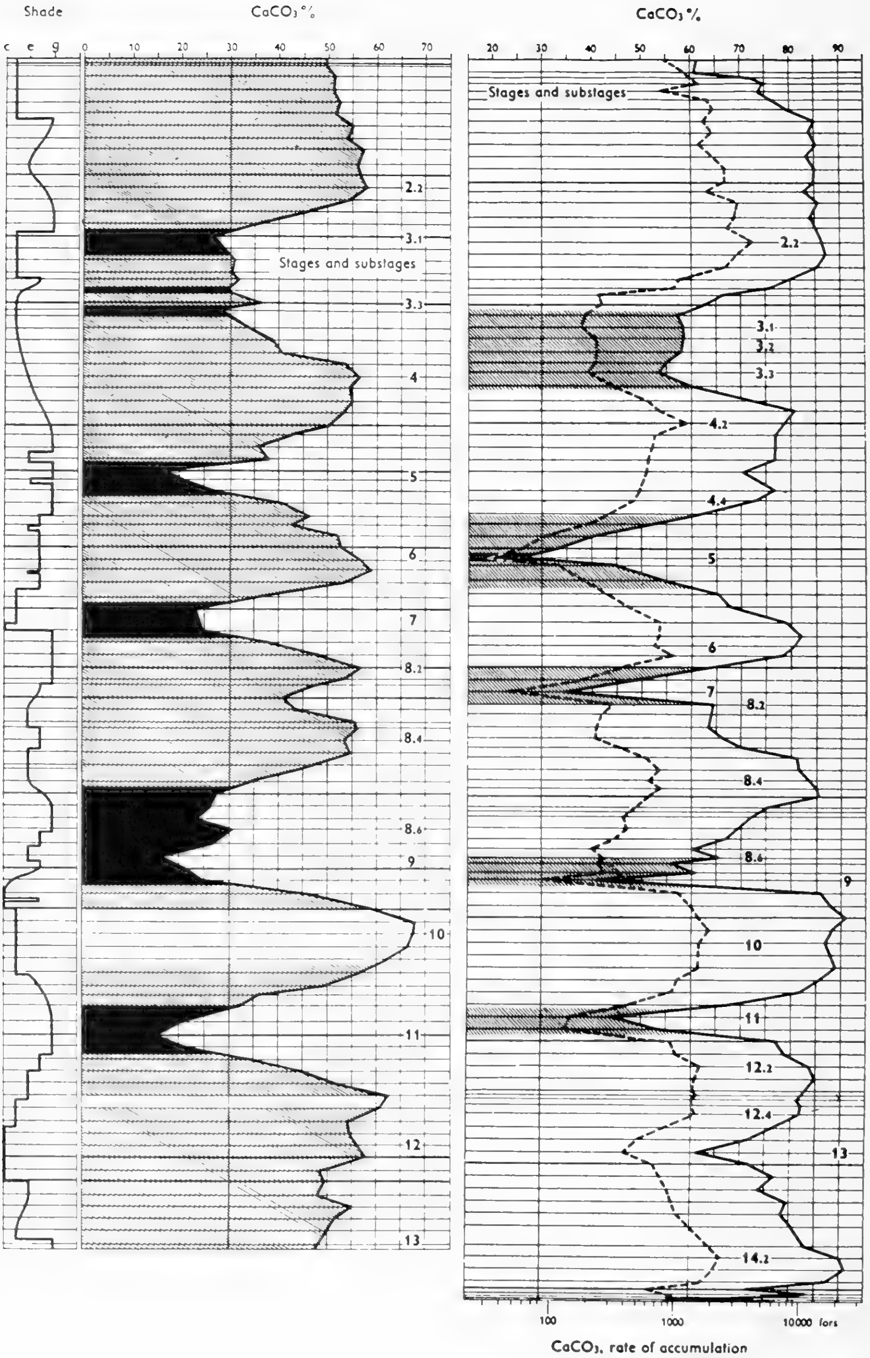


Fig. 3. Relative rate of accumulation of barium in the Postglacial stratum of the profile shown in Fig. 2 (Goldberg and Arrhenius, 1958).

during which a position of the North Pole in the North Pacific has been postulated. As Walter Munk has pointed out, this is one of the most interesting applications that can be thought of for some of the drilling tests planned to precede the ultimate attempt for penetration of the earth's crust.

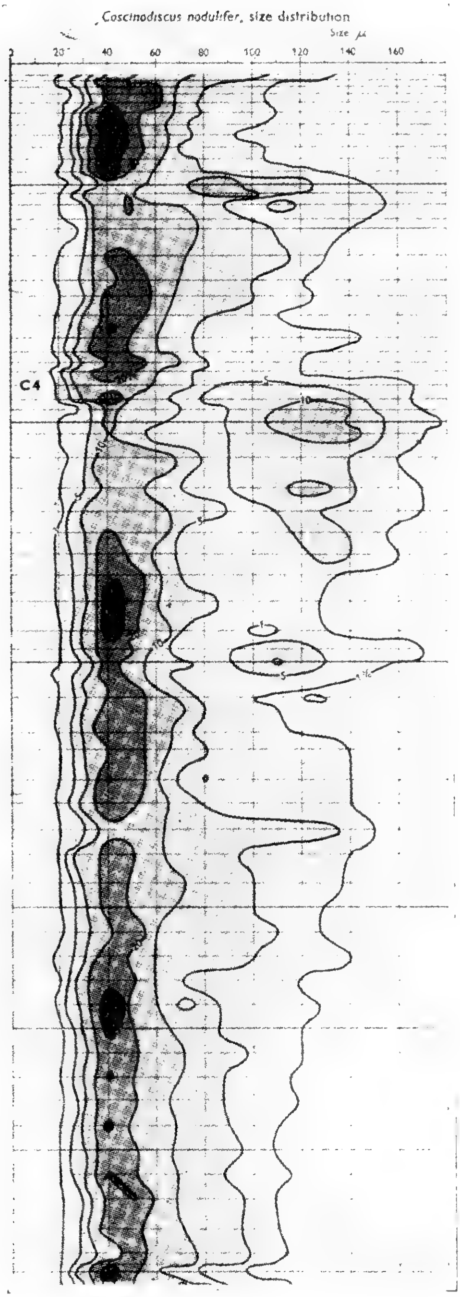
So far the meridional cross section through the sedimentary strata under the equator, shown in Fig. 2, has been used to demonstrate the possibilities for accurate mapping of polar wandering; however, another interesting feature of the equatorial sedimentation mechanism should also be pointed out. If, instead of investigating the relation between latitude and accumulation, we focus our attention on the variation in time of accumulation of biologically produced materials such as skeletal material of carbonate, silica, or phosphate, or elements such as the rare earths, or zirconium, we find (Fig. 4) that there is a marked variation with time in the amount and kind of organic remains, in the cases shown here, of calcium carbonate and diatomaceous silica. This sequence is repeated in detail along the equatorial strip of high productivity; the section shown in the middle is from north of Marquesas; the one to the left shows the conditions found 5400 km further to the east at the Galápagos Islands. Westward this stratification can be followed to near the date line, and altogether it extends along the equator over nearly one-quarter of the earth's circumference.

The present time is characterized by a relatively low carbonate content in the sediment whereas during the preceding age, which coincides in time with the last glaciation in higher latitudes, the contribution of organic remains was high. Going downward in the sediment, four or five major maxima of this kind and a number of smaller ones are encountered before the Tertiary boundary is reached, identified by Emiliani on the basis of the markedly higher paleotemperature of planktonic Foraminifera. It has been demonstrated by Bramlette that this change in temperature coincides in time with an evolutionary change in the coccolithophorids, which is recognizable over the equatorial Pacific and probably also elsewhere. The Tertiary strata are characterized by smaller amplitude of the variations in the supply of organic remains to



(*a*) (*b*)

Fig. 4. (*Continued on facing page.*)



(*c*)

Fig. 4. Carbonate concentration as a function of depth in Equatorial Pacific sediment cores from (*a*) 106°W Long and (*b*) 135°W Long, and (*c*) size frequency distribution of the diatom *Coscinodiscus nodulifer* in the latter core (Arrhenius, 1952).

the sediment, and a lower average carbonate content, indicating a general decrease in the productivity.

It has been demonstrated by Emiliani that the strata formed at increased productivity in the equatorial Pacific are associated with colder surface water, as indicated by the oxygen isotope ratio in planktonic Foraminifera. He has also shown that during each given time period the surface temperature of the ocean drops toward the equator, consistent with the upwelling of cold deep water there, and that this temperature gradient becomes steeper during periods of high productivity (Fig. 2, top graph).

All these observations strongly suggest that the periods with a high rate of accumulation of organic remains were periods of increased rate of vertical water transport in the equatorial divergence, which ultimately appear to be caused by increase in the trade wind intensity. The ocean sediments thus provide us with a record not only of polar wandering but also of the intensity changes in the low-latitude atmospheric circulation, which is directly tied in with the great climatic changes that during the last geological period resulted in the ice ages.

The direct effect of cooling of the surface water at intermediate latitudes has also been traced over large areas in the Atlantic Ocean and in the Mediterranean through the original work by Schott (1935) on species of Foraminifera, sensitive to cold and warm water, followed by a number of similar studies by Cushman and Henbest, Phleger, Ovey, Ericson, and others. Quantitative information on the temperature development has been provided by Emiliani's (1955) extensive studies of the paleotemperature as indicated by the oxygen isotope ratio in tests of planktonic Foraminifera. Again it is here evident that the last period of cooling coincides in time with the last ice age, and by inductive reasoning it seems safe to assume that the previous low-temperature periods correspond to the older ice ages. The reason why this is difficult to prove directly is that the time scale of these events, as they are recorded on the continents, is only approximately known.

It should be mentioned in this connection that Emiliani (1955) has attempted to correlate the succession of cold and warm periods as reflected by the paleotemperature in Atlantic sediments, with the periodic changes in distribution of solar radiation over the earth, postulated by Milankovic as responsible for the glaciations. The time lag observed between temperature minima and the maximum extension of continental ice sheets has recently been explained by Emiliani and Geiss (1959) on the basis of plastic flow of the ice. With the more accurate measurements of geological age in the range of a few hundred thousand years that are promised by the ionium-thorium method which is now being perfected by Goldberg and co-workers, and by the protactinium method which is being developed by Rosholt, Sackett, and Koczy it should be possible to check Emiliani's theory accurately.

In spite of our still limited knowledge of the sediments covering the deep ocean floor and in spite of the ambiguities attached to the time scales, which so far have been extrapolated from carbon-14 measurements in the surface layer, it is probably right to say that our best quantitative information about the climatic evolution of the earth during the last million years comes from the oceanic record. An exception has to be made for the last 20,000 years, which are known in greatest detail from continental sediments, where the record has in this case not been disturbed by later catastrophic events.

Among recent geophysical hypotheses, inspired by observations on the deep ocean floor must also be mentioned the one proposed by Ewing and Donn (1956) attempting to explain the climatic oscillations in our geological period, and their commencement about a million years ago. Ewing and Donn were impressed by the indications in Atlantic cores of sudden transition from low surface water temperatures, typical of the glacial ages, to the conditions prevalent now and during interglacial ages. They assume that the location of the pole in the Arctic basin gives rise to a climatic instability and self-sustained oscillations. An originally ice-free Arctic Ocean, freely exchanging water with the Atlantic would be an efficient source of moisture in the Arctic region, causing growth of the continental ice sheets. The tying up of water in these ice sheets, however, would lower the sea level to near the sill depths of the Arctic basin, and the lowered influx of warm, Atlantic water together with the cooling from the inland ice over North America, northern Europe, and part of Siberia would lead to the sudden freezing over of the Arctic Ocean. The source of nourishment for the ice sheets and glaciers would thereby be sealed off, and they would start to wane and return their water to the ocean; the sea level would rise above the effective sill depth, the influx of warm water from the Atlantic would be increased, the ice cover over the Arctic Ocean would vanish, and the cycle could start over again.

Some authorities have questioned the assumption that there is really a lag effect in the system, causing it to overshoot, and leading to self-sustained oscillations rather than to a steady state. Also, it has been debated whether the heat effects involved would be sufficient. The hypothesis, however, possesses another interesting feature, namely, that it can be checked experimentally. To explain the start of the series of oscillations mentioned, Ewing and Donn (1956) assume that the North Pole in Tertiary time was in the Pacific Ocean, that is at least thirty degrees away from its present position, and that the first ice age occurred as a result of the motion of the pole into the Arctic basin. It must be said that such a motion is indicated neither by the numerous Tertiary sequences available from the Pacific Ocean floor, nor by paleomagnetic measurements, however, further evidence for or against the theory could probably be obtained from cores about 20 m long in the Pacific equatorial zone; this is within the reach of present coring methods.

The density of solid particles in the atmosphere and in the space between us and the sun has attracted great interest as possible variables in the past, responsible for climatic change and other phenomena, and again, the best record of worldwide or large-regional changes in source, path, and amount of such particles seems to be the ocean sediments. Singular events like volcanic eruptions are of special interest, as they provide us with useful stratigraphic marking horizons. The Late Glacial eruption in Laacher See in Germany is a famous example in which the ash spread over large parts of Northern Europe making it possible to recognize the Alleröd interstadial during which the eruption happened. In Iceland the archeological development is tagged by widespread ash layers, and in Patagonia the local records of the

Late Pleistocene climatic development in peat bogs have been correlated by interstratified ash layers from the Andean volcanoes. Correns (1937), in his work on equatorial Atlantic sediments, noted the variability in the volcanic components, and in the Mediterranean a great deal of interest has been devoted by Mellis, Pettersson, and Norin (1958) to identification of observed ash layers in the sediments with known historic or prehistoric volcanic events. The first and so far perhaps most successful attempt at oceanwide correlation of ash layers in long sediment sequences was made by Bramlette and Bradley (1942) in the cores raised by Piggot between Newfoundland and Ireland (Fig. 5). These results offer a powerful tool for correlation of the numerous long cores which since have been raised in the North Atlantic, and for reconstruction of the volcanic history of the whole region.

One of the most dramatic discoveries of this kind is the recent finding by Worzel (1959) of extensive ash beds in sediment cores near the South American coast (Fig. 6) all the way from Peru to Mexico. In their preliminary description of these strata, Ewing, Heezen, and Ericson (1959) interpret them as one continuous unit, which would represent a single gigantic eruption. One would, however, under these conditions expect to encounter the layer also in the more slowly accumulating sediments further out in the equatorial Pacific, reworked and spread vertically by bottom organisms (Fig. 7) and perhaps altered to montmorillonite but still mineralogically discernible. In these cores, including one from the Galápagos area, not far away from the Worzel ash in the Bight of Panama, however, several minor concentrations of unaltered ash of different types, and of montmorillonite are found, but nothing of the dimensions observed near the coast. It appears, therefore, that at the present time caution should be observed in the correlation of the coastal ash layers, that might well be derived from a series of eruptions from different volcanoes in the Cordillera.

While the volcanic dust appears as spikes in the sedimentary record, there is a fluctuating continuum of airborne detritus carried out over the oceans (Fig. 8) and deposited there, especially from the arid lands of the world. This dust has quite a varied mineral composition. One of the major components which is easily deter-

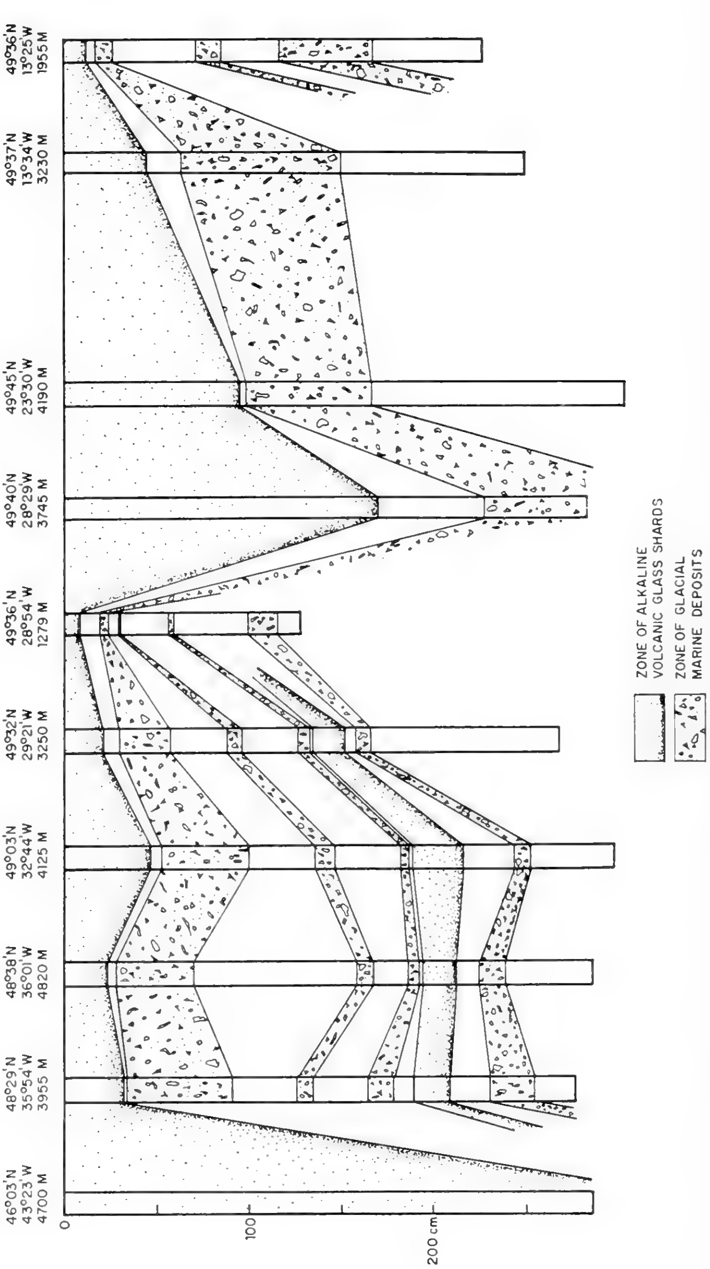


Fig. 5. Lithology of North Atlantic sediment cores, showing zones with glacial marine deposits and with alkalic volcanic glass (Bramlette and Bradley, 1942).

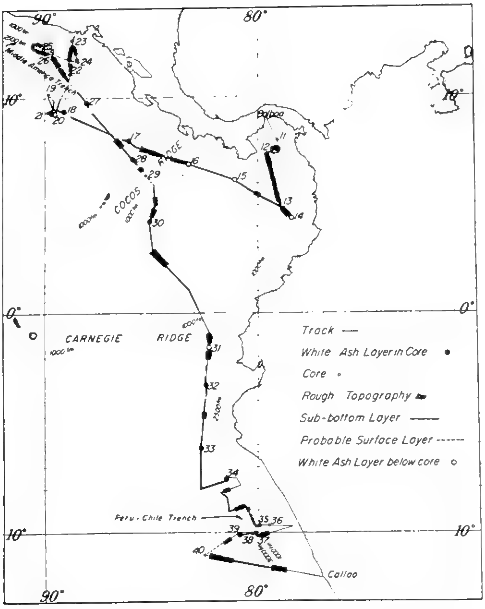


Fig. 6. Stations where an ash layer was sampled by the piston corer are shown by filled circles. Heavy lines indicate those parts of the track of the *Vema* along which a subbottom layer was recorded by the echo sounder. Ewing, Heezen, and Ericson have assumed that the subbottom reflection is caused by volcanic ash, and that this forms a continuous layer with a minimum extent over the area shown in the figure (Worzel, 1959).

mined, namely quartz, has been studied in some detail in the Pacific and shows a distribution of considerable interest.

Investigations of the size frequencies of the quartz particles in pelagic sediments (Fig. 9) showed a high degree of sorting, a mean diameter in fine silt, and an unusual cutoff of the very small particle sizes indicating an eolian origin of the material in several cases. Subsequent measurements by Goldberg and Rex (1958) support this view in several independent ways, and indicate the existence of two zonal maxima, in each hemisphere around 30° Lat, with a markedly increased content of quartz in the form of fine silt (Fig. 10). Goldberg and Rex have ascribed these maxima to fallout from the jetstreams which with high wind velocities circle the globe in these two latitudinal zones on the border between the stratosphere and the troposphere. The difference in intensity

Fig. 7. Vertical section through the top eight centimeters of a sediment core from the East Equatorial Pacific, showing the mixing of material from adjacent strata by the activity of mud eating animals. Measurements of the amount of foreign material present at each level demonstrate that, assuming an originally sharp boundary between the light and dark sediment units, 2–3 cm thick layers below and above this boundary will ultimately contain 50 percent of material originating from the other side of the boundary. The drop of concentration of material originating from a given level with increasing vertical distance from this level is rapid; in only a few cases have single worm channels been observed to penetrate more than 20 cm (Picciotto and Arrhenius, unpublished).

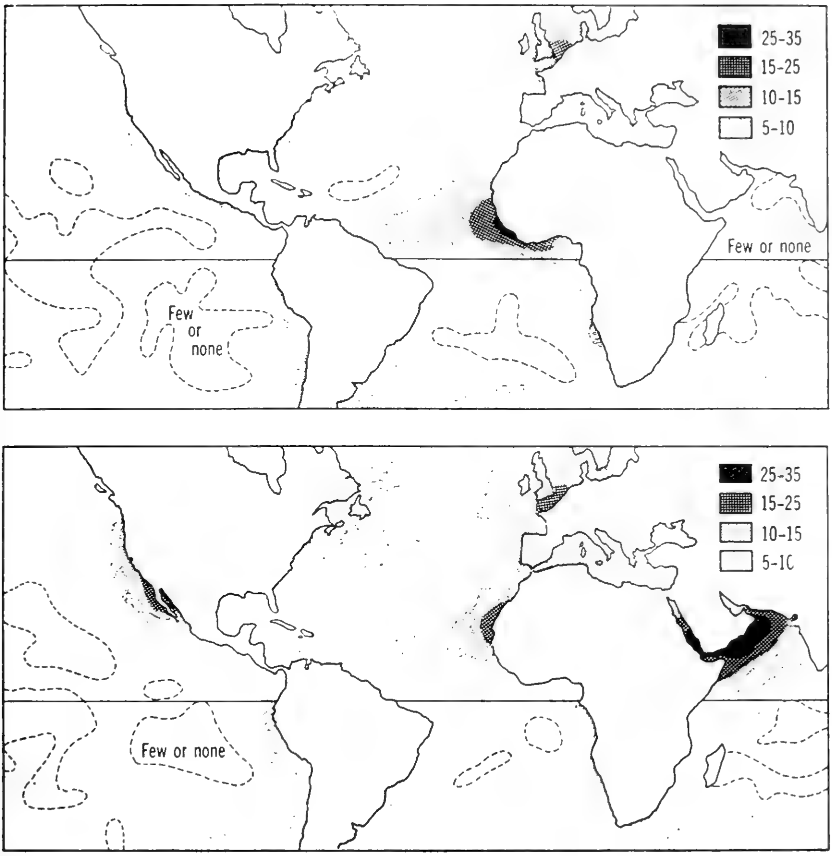


Fig. 8. Average frequency of haze (solid aerosol) during northern winter (upper graph) and summer season (lower graph). The extensive transport of dust from the African continent and the Arabian peninsula is clearly reflected, and the importance of the Sonoran and Andean deserts as supply areas for the Pacific sediments is indicated. The haze area in northwestern Europe is probably due to industrial smoke production (Arrhenius, 1959a).

of the quartz maxima in the Northern and Southern Hemispheres is, according to the same authors, due to the smaller areas of arid lands in the Southern Hemisphere. In addition, it appears that the distance from the coast has an important effect on the rate of fallout of quartz and other windborne minerals.

The concentration values of up to 20% quartz in the northern

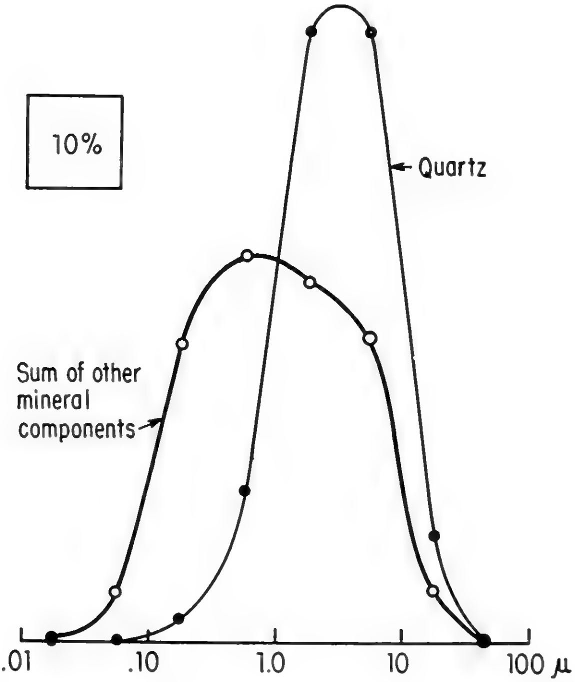


Fig. 9. Size frequency distribution of quartz and of the sum of other mineral components in a clay sediment from the north equatorial Pacific (Arrhenius, 1954, unpublished).

maximum suggest a total contribution of windborne minerals to the pelagic sediments in this zone of perhaps twice this value, and emphasize the quantitative importance of eolian components in some pelagic sediments. Strangely enough, no significant variations in this contribution have been found between the glacial and interglacial stages. The Tertiary sediments in the north equatorial Pacific, however, are low in quartz, indicating smaller arid source areas, or less efficient transport, and in the upper Pliocene a gradual transition is found from this situation to present-day conditions.

The importance of accretion of cosmic dust and micrometeorites was realized during the first extensive investigations of deep sea sediments by Murray and Renard (1891) after the *Challenger* expedition during the last century; however, it was left to the

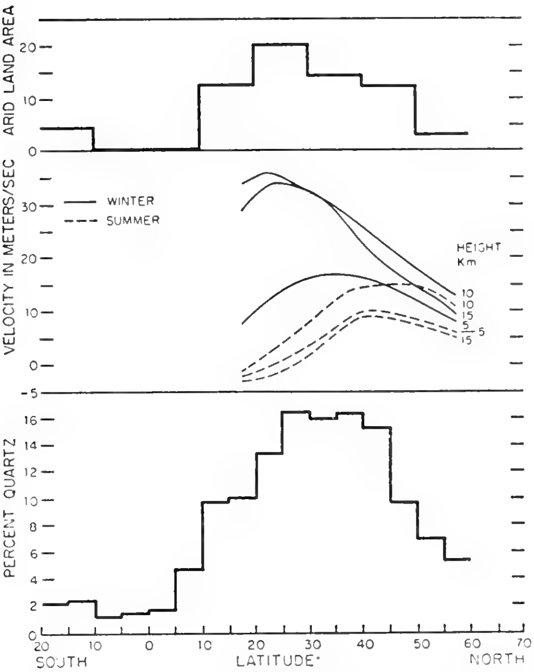


Fig. 10. Meridional distribution of quartz in east Pacific sediments (lower graph), velocities of high altitude winds (middle graph), and arid areas of the world (top graph) (Goldberg and Rex, 1958).

initiative of Hans Pettersson to start a quantitative study of the concentration and distribution in time of the microscopic spherules of nickel iron which form the perhaps most easily concentrated and identified component of cosmic material in deep sea sediments. Thanks to the technique developed by Kullenberg (1947) and employed by him during the Swedish Deep Sea Expedition large-diameter cores were available which permitted the collection of statistically significant numbers of spherules from sufficiently narrow depth intervals (Fig. 11). The results obtained by Pettersson, Fredriksson (1958), and Laevastu and Mellis (1955) indicate an increase in concentration of cosmic spherules in the Recent strata, which is interesting in view of the hypothesis that meteorites have started to reach the earth in increasing numbers in historic time. This distribution has been found both in the Pacific

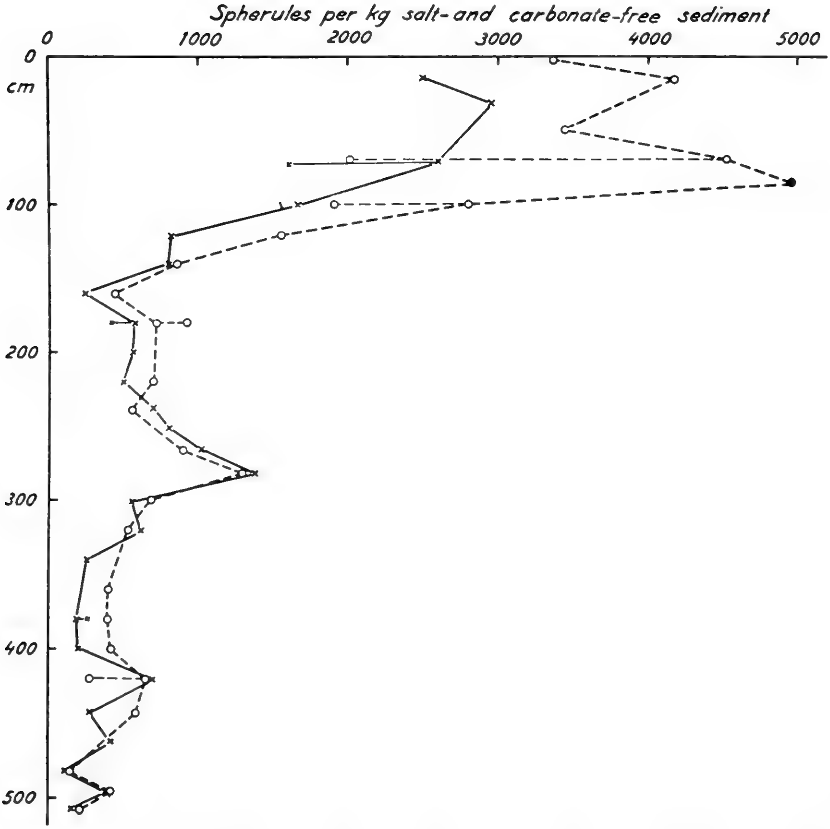


Fig. 11. Concentration of cosmic spherules in a sediment core from the West Pacific. The different curves represent results obtained by slightly different methods of assay (Pettersson and Fredriksson, 1958).

and the Indian oceans; in addition, several significant minor variations are found in older strata. Radiocarbon data, combined with stratigraphic measurements, appear to confirm that the recent increase in the concentration of cosmic spherules is due to an increase in their rate of accretion on the earth rather than to dilution with a larger amount of other sedimentary components.

The original idea by Murray and Renard (1891) that the spherules are solidified droplets of molten iron splashed off from meteorites entering the atmosphere has been further corroborated through elegant microradiographic analyses by Castaing and

Fredriksson (1958) and Fredriksson (1958). Still nobody has been able to establish the rate of accretion on the earth's surface of fine cosmic dust that might be of great geophysical significance. Silicate chondrules like those in meteorites have, however, been observed by Murray and Renard, and recently by Bramlette. An interesting possibility for estimating the amount of cosmic dust settling on the earth may be offered by the fact that the meteorites, in contrast to terrestrial rocks, are reported to contain considerable amounts of monoclinic magnesium-iron pyroxenes, clinoenstatite and clinohypersthene, which are relatively easy to concentrate, and which belong to a series of minerals which do not readily decompose on the ocean floor.

In a survey like this it has been necessary to limit the subject to an impressionistic account of a few topics. It is impossible to give justice, under such conditions, to all the interesting work that has been done in the field, and to point out all the fascinating possibilities that are now apparent. I hope, however, that I have been able to convey a general impression of the wealth of information that the pelagic sediments offer to those who devote themselves to quantitative study of the past history of the solid earth, its ocean and atmosphere, and its interrelation with outer space.

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II. Populations of the Sea

Paleobiogeography of the Marine Realm*

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> In studying the geographical distribution of organized beings philosophically, it is absolutely necessary to call in the aid of geology.—Edward Forbes and Robert Godwin-Austen (1859, p. 9).
>
> The picture cannot be painted in black and white when nature has neither, but only infinite gradations of darker and lighter gray.—George Gaylord Simpson (1952, p. 164).

THE ultimate aim of biogeography is to express and interpret the dispersal of the individual components of the biosphere through the filter systems of physical geography and environment and their organization into distinctive, areally limited communities, provinces, and realms.

It is self-evident that, in order to survive as more than an ecologic or evolutionary curiosity, a species must be able to migrate, to install itself in new locations, to mature and reproduce there, and to adapt itself to local conditions of existence over a sustained interval of time. The degree to which different organisms do this summarizes the ecologic vitality of the species and is the best measure of success in the basic competition of all life for a larger measure of the total energy supply. The patterns created in the struggle for perpetuity are the essence of descriptive biogeography and paleobiogeography, which necessarily precede all useful efforts toward interpretation.

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These static patterns, moreover, have dynamic and historic causes of such complexity that only the boldest have dared confront them, and they too commonly with extraneous and weakly documented hypotheses—frequently repeated in substantiation of themselves after cycling through other and unfamiliar disciplines. The results of such circular reasoning are well illustrated by various *ad hoc* land bridges, whose unbridled rising and sinking in the late nineteenth and early twentieth centuries explained alike the similarities of geographically distant biotas, and the dissimilarities of neighboring ones, both at sea and on land. Handlirsch (1937) and Schmidt (1955) have effectively demolished the general application of this now diminishingly popular mechanism (see Croizat, 1958, for the opposite view), which, for the moment, merely illustrates the need for verifiable interpretive principles and generalizations.

Modern marine biogeography at least has the advantage of recognized ancestry (Forbes, 1844; Schmarda, 1853; Forbes and Godwin-Austen, 1859; Regnard, 1891; Ortmann, 1896; Petersen, 1914, 1915a, b; Ekman, 1953; Pérès and Picard, 1955; Pérès, 1957; Hedgpeth, 1957b-d). Even the parentage of paleobiogeography is obscure, however.

D'Orbigny, who was more sensitive to the qualities of his legitimate scientific children (Heron-Allen, 1917), devoted two pages of his famous *Cours élémentaire*, etc. (1849, Pt. 1, pp. 6–7) to stressing the importance of knowing all about the conditions of existence, only to conclude (*op. cit.*, 1851, Pt. 2, (1) p. 241) that "Depuis le commencement du monde animé jusqu'aux derniers étages des terrains tertiaires (sic), on voit . . . une répartition uniforme des êtres tout à fait indépendante des lignes isothermes actuelles, et . . . toujours la faune tropicale"—a paleontological part truth that to some degree still encumbers paleobiogeographical inquiry.

Neumayr (1883, 1885) subsequently reached a contrary conclusion from his global analysis of the Jurassic faunas, delineating climatic zones comparable to those of the present day. Although Neumayr's zonation has since been discredited in detail by Uhlig (1911) and Arkell (1956, pp. 615–618), these authors agree that there was at least a broad climatic zonation roughly parallel to present latitudinal belts in Middle and Late Jurassic time; and fluctuating climatic zonation parallel to the present equator is now widely accepted for the Cenozoic and late Mesozoic (see Durham, 1959, for a recent summary). For Paleozoic time in general the question is still moot, and much additional work will be needed to resolve it.

Johannes Walther laid the basis for subsequent expansion of marine paleobiogeography as a distinct empirical discipline with his *Einleitung in die Geologie als historische Wissenschaft* in 1893–1894, and many paleontologists and geologists since Neumayr and Walther have constructed paleogeographic, or, more accurately, shoreline maps, utilizing various combinations of geologic and paleobiologic evidence. Recent activities in marine paleobiogeography are exemplified in stimulating papers by Caster (1952), George (1958), Minato (1953), Ager (1956), and Davis and Elliott (1957)—named in stratigraphic sequence. The summary account by Davis and Elliott on the early Eocene London clay sea deserves special notice, both because of the wealth of information available and for the skill and balance with which these authors utilized it to reconstruct the living conditions and biogeographic affinities of this classic sequence.

Growing interest in the fundamental aspects of paleobiogeography is reflected by the synthetic works of the Termiers (1952, 1957, 1959; Wells, 1953) and by the fact that the first session of the Soviet Union's All-State Paleontological Society in 1955 was devoted to "Problems of paleobiogeography and biostratigraphy" (Stepanov, 1957). On the western side of the Atlantic, the paleobiogeographic data are one of many ingredients of the U. S. Geological Survey's program to produce a series of paleotectonic maps, which will summarize the historical development from Cambrian onward of sedimentation, biotal migration, and crustal movement within the continental United States (McKee *et al.*, 1956, 1959).

The pressing need, as in most empirical disciplines today, is for a clear sequence of integrative principles that will strike more directly and surely through the growing clutter of facts to the yet distant treasures beyond. The cycle is a vicious one for, generally speaking, large masses of data must still be assimilated, organized, and correctly interpreted on regional or worldwide scales before the essential principles can be confidently formulated or the unique explanation deduced for any given set of local or temporary conditions. This should not deter us, however, from formulating, as best we can, such working principles as will give structure to existing knowledge and direction to new research.

General Limitations of Paleobiogeographic Evidence

Paleobiogeography is no exception to the rule that all constructions of the mind are beset by two groups of limiting factors, human and objective.

Because thought processes are complex and language is linear, the mental image of one mind cannot be conveyed instantaneously and unerringly to another except in some forms of mathematical expression, which do not apply generally to the complexities of the biosphere. An imperfect means of communication at best, language may become perversely irrational in relation to facts or concepts with which one is emotionally involved. Weak arguments may then be bolstered with unwarrantedly strong statements, and, by way of compensation, strong probabilities may be stated with uncalled for reserve. This is the involvement paradox (Fig. 1) manifestations of which include the dubious use of expressions such as *must be*, *doubtless*, and *obviously*—warning flags that invite both reader and writer to reconsideration of the evidence. The more interpretive the subject the more prevalent the effects of the involvement paradox, and the focal problem of paleobiogeography (and paleomagnetism) is the highly interpretive subject of the former arrangement and orientation of the earth.

Objective factors affecting the application of paleobiologic evidence to paleobiogeographic problems are both external and internal, but all are expressed and controlled by the broad external conditions of geographic range, habitat variation, and time. The general effect of these conditioning factors on the applications of the evidence is roughly indicated in Fig. 2, where paleobiogeography stands, within the matrix of evolution, as the intermediate

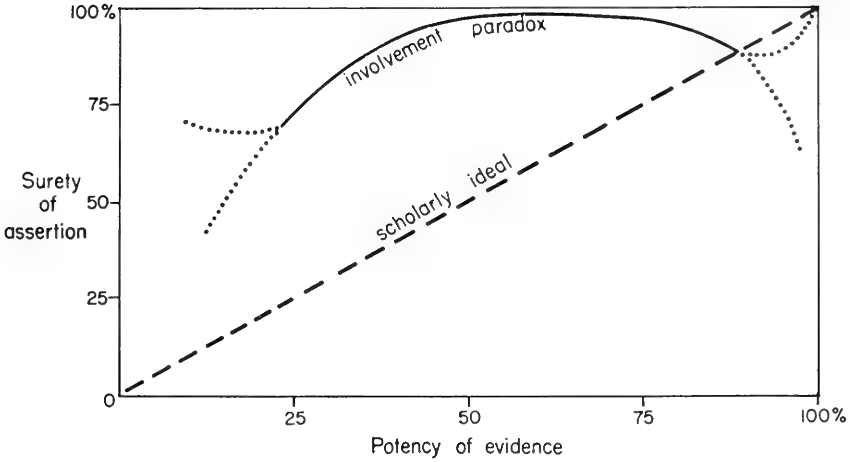

Fig. 1. Human factor in communication.

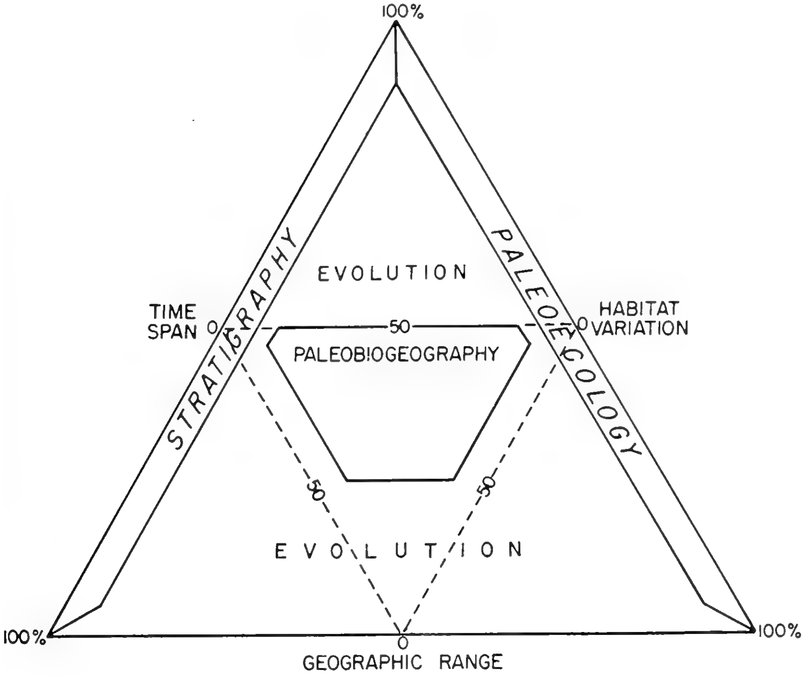

Fig. 2. External conditions affecting the application of paleobiological data.

keystone of the pyramid described by the long- and wide-ranged, ecologically restricted biotic elements that make the best paleoecologic indicators, and the wide-ranged, facies-crossing forms of short time span that are favored for stratigraphic markers. Paleontology in practice is not so simple as that, but it is a fact that a wide range of intermediate geographic and habitat characteristics is of interest for paleobiogeography, provided the species are not too ubiquitous; and provided the ecology, evolutionary sequence, and time dimension can be supplied by other forms.

No biogeographic or paleobiogeographic conclusions are any better than the data and interpretive principles on which they are based, so an accurate and refined systematics and a knowledge of the geographical distribution of modern organisms are at the base of the pyramid. Without this foundation the structure floats in thin air. To assume, for instance, as some have done, that wide geographic separation excludes the prospect of systematic identity is to bias the data. It is only by critical analysis of objective similarities and differences between biotas, in context with the inferred relations of land and sea and the paleoecologic implications of the enclosing sediments, that useful concepts of migration routes and dispersal mechanisms can be evolved for comparison with the land connections, current systems, and regional climatologic variation demanded by given earth models.

Distribution of Marine Organisms

According to the basic geological principle of uniformitarianism,* which uses observable and testable processes and dynamic relations as the keys to past events, the interpretation of marine paleobiogeographic data is based on analysis of the mechanisms that affect the survival and dispersal of organisms and organic remains in the present seas (Fig. 3). Given a particular set of geographic, climatologic, and historic conditions, the variables involved are of

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* Uniformitarianism is not to be confused with gradualism, or thought of as properly incorporating purely static analogy, a misconception that has led to uncritical rejection of this fundamental operational principle, without which geology cannot be thought of in scientific terms. It does not exclude catastrophic processes or unusual events, but only *ad hoc* reasoning.

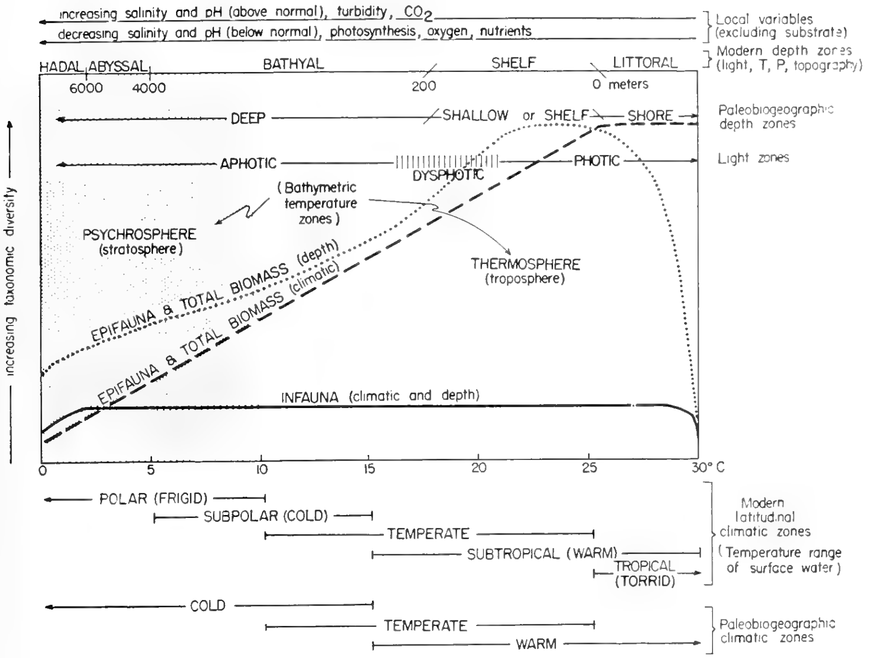

Fig. 3. Principal external variables affecting the distribution of marine biotas.

three kinds: external, internal, and cobiotic. External factors are those of the physical and chemical environment; internal factors are those that exist within, and are an integral part of, the organism itself; and cobiotic factors are those introduced by the rest of the contiguous biosphere, including that part of the biosphere which may live within, consume, or destroy the dead remains of the organism in question. The response of the organism to these variables is expressed in its adaptive and competitive characteristics and ultimately in its range in environment, space, and time. The biotal composition of a given area or habitat at a given time is a composite function of metabolic intensity and rate of evolution (e.g., Bray and White, 1954, pp. 83–84), duration of biota and environment (e.g., Fischer, 1960, p. 80), and intrinsic characteristics of environments and organisms. The limiting conditions of existence for a particular species at a given place may involve any of those obtaining at the time of, or before, its existence. The principal influences that affect the biogeographical characteristics of the organic community or biome, however, are those major external variables that undergo the maximum fluctuation (e.g., Jones, 1950, p. 299).

External Factors of Existence

External factors influencing the geographic distribution of the marine biotas are, of course, vastly different from those at work above sea level. Water is heavier, more viscous, a much poorer heat conductor, a far superior heat reservoir and transfer system, and has a far lower gaseous oxygen content and higher freezing point than air. Ocean water is richer in most kinds of dissolved solids and has a far more uniform composition than fresh water. Migration routes for land animals are likely to be barriers and isolating mechanisms for marine ones.

Let us look at the principal external variables that influence the distribution of marine biotas under given geographic, climatologic, and historic configuration. In Fig. 3 the systematic variables define major biogeographical provinces or zones; local variables are shown at the top. Forbes and Godwin-Austen (1859, p. 17) recognized these same variables a century ago when they stated: "The distribution of marine animals is primarily determined by the influence of climate or temperature, sea-composition and depth, in which pressure, and the diminution of light are doubtless important elements." Plants do not fit the same detailed scheme, but they are equally subject to the three basic variables, sunlight, temperature, and salinity.

Sunlight, of course, is the primary source of radiant energy that impels the whole earthly biosphere and is responsible for all but a minute fraction of its available heat budget. Together with the earth's trajectory and rotation, and the pull of the sun on its equatorial bulge, sunlight determines the latitudinal climatic zones, which designate by other words the amount of local available energy. It determines the vertical division of the hydrosphere into photic, dysphotic, and aphotic zones, which can also be expressed in terms of photosynthesis, oxygenation, and temperature.

Temperature, which is effectively one expression of light, provides us with the most concrete basis of biogeographic subdivision and the most convenient circumglobal terms. Global temperature and temperature zonation has, of course, varied in the past, from causes both terrestrial (e.g., Plass, 1956) and extraterrestrial (e.g., Brooks, 1951, pp. 1016–1017); and, for the paleobiogeographer, it is essential not to confuse temperature subdivisions with geodetic terms such as tropical, polar, or equatorial. The sequence warm, temperate, and cold, with the temperature ranges indicated (Fig. 3), describes the local conditions and biotal affinities as closely as the paleobiogeographer can usually recognize them, and without commitment as to orientation, subsequent movement, and geodesy. In paleobiogeography also it is rarely meaningful to attempt to approximate depth zones more closely than shore, shallow, and deep, with *deep* as here used including everything below the photic zone (or "wave base"). Quantitative depth and temperature limits naturally should be estimated wherever the evidence permits, but the usual kinds of paleontological and sedimentological evidence are apt to limit depth evaluation of ancient seas to more ambiguous terms such as shelf, shallow shelf, deep shelf, shallow slope, deep slope, basin, or shore zone. The limiting effects of temperature and other variables may affect the organism differently at different stages of existence; Hutchins (1947) showed how upper and lower seasonal temperature limits on installation and survival produce four basic types of latitudinal zonation of interest to zoogeographers.

Salinity affects the inhabitants of the hydrosphere through osmosis and secondarily through density, light penetration, pH, and the distribution of mineral nutrients. The effects of salinity variations in the older Tertiary of the Fergana Gulf were described at this Congress by Hecker, Ossipova, and Belskaya (1959).

The distribution of life in the marine realm under conditions existing at any given time is a reflection of the variables mentioned, plus depth, pressure, gas content, and turbidity of the water and substrate conditions. The paleobiogeographer has only the fossils and the enclosing sediments, which may or may not have been associated in life. He must deduce the rest from the biological characteristics, regional distribution, and evolution of his fossils, and from the geochemical, mineralogical, textural, and structural characteristics of his sediments.

It is gratifying to know, therefore, from contemporaneous biogeographic and ecologic research that there are distinctive patterns in the variety, numerical abundance, sizes, and even shapes of organisms that denote trends, if not specific points, in the external environment of the life assemblages concerned (Clements and Shelford, 1939; MacGinitie and MacGinitie, 1949; Allee *et al.*, 1949; Jones, 1950; Ekman, 1953; Hedgpeth, 1957a; Fischer, 1960). The curves shown in Fig. 3, to be sure, are only a caricature of the changes in relative taxonomic variety (including variety but *not* bulk of total biomass) that accompany changes in the external variables, but they do suggest their general shape. We owe to Petersen (1914, 1915a, b) and Thorson (e.g., 1957) the emphasis on the great variation displayed by the epifauna, and to some extent by the nekton and plankton, as contrasted to the intrinsically less varied infauna (*in* the substrate, not the endofauna, which includes internal symbionts). This difference reflects the closer interrelations of the epifauna with external climate and associated plant and animal communities. If it were not known, it would have been logical to deduce that the infauna occupies the ecologic realm of least variation and greatest stability.

I have summarized elsewhere (Cloud, 1959b, p. 931) the paleobiogeographically useful and well-known gradients in variety, abundance, and size with temperature, salinity, and depth, and these are discussed in articles by several authors in Hedgpeth (1957a) and by Jones (1950). It will suffice here to underscore that these gradients are broadly similar in kind and are to be distinguished primarily on the basis of abruptness of variation, associated changes in morphology and composition of the biotas, and sedimentological evidence, including that from isotopic and geochemical methods.

In general, however, the paleobiogeographer is safe in concluding (Fig. 3) that great biotal variation is presumptive evidence of warm, shallow seas of normal salinity and that widespread faunas of limited variety and relatively persistent composition (and commonly large numbers of individuals) are likely to represent waters that were cold or deep, or both. Limited variety and abruptly changing composition of biotas implies local salinity deviations, especially if the biotas include a relatively large proportion of internally stable or homoiosmotic organisms such as fishes and some crustaceans, and exclude internally variable or poikilosmotic forms, such as echinoderms, cephalopods, brachiopods, bryozoans, and corals.*

Internal and Cobiotic Factors of Existence

Internal variables affecting the geographic distribution of marine organisms include their individual metabolism and mobility, frequency and range of movement, manner of and adaptations for movement or fixation, sensory responses, size and specific gravity, mode and time of reproduction, and length of larval life. To these should be added their adaptability to variations in the physical, chemical, and gaseous conditions of the external environment; their reproductive lability; and their evolutionary intensity, which is a function of metabolism, rate of change, and time.

The cobiotic factors include all facets of competition for the available energy resources—light and mineral nutrient absorption by the photosynthesizers, nature of and availability to the organic nutrient supply by the heterotrophs, predation, symbiosis, and degree of occupancy of available ecologic niches.

The internal and cobiotic factors have important effects on the numbers and individual survival prospects of the various categories of organisms, as roughly indicated in Fig. 4, a scheme inspired by the work of Blegvad (1915) and by Imbrie's (1959) contribution to this Congress. Size, reproductive characteristics, and competition are not specifically included in this diagram. Number of offspring, however, decreases, and size of individual, length of

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* By convention, the widely employed prefixes *poikilo* and *homoio* designate marked *internal* variation vs. little or no variation, whereas *eury* and *steno* refer to *external* tolerance. A homoiosmotic organism is also euryhaline because its ability to regulate the salinity of its body fluids permits it to survive a wide range of external salinities. A poikilothermal animal is characteristically stenothermal in habitat tolerance, because its inability to regulate body temperature is deleterious under wide external temperature variation.

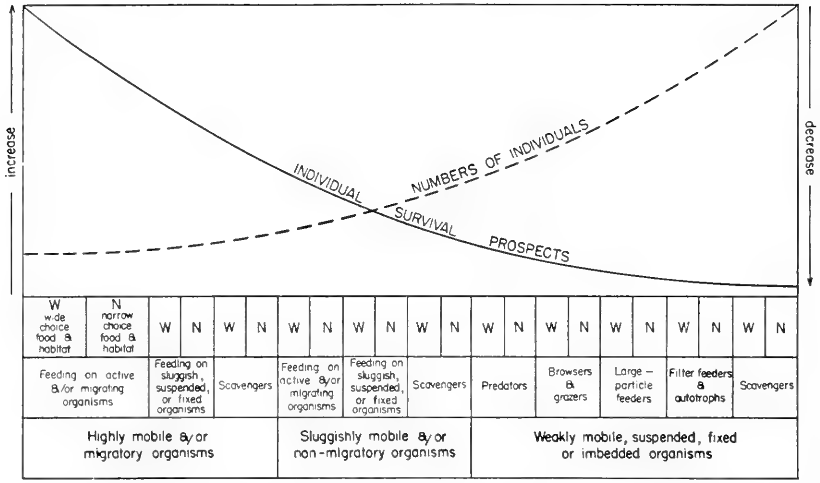

Fig. 4. Numbers and individual survival prospects of marine organisms regulated by different internal and cobiotic factors.

parental dependency, and degree of parental care in general increase toward the left, with decreasing size of the breeding population. Competitive factors are involved throughout. Moreover, an important paleobiogeographical exception to the direction of size increase is provided in the case of the shelled invertebrates. Other factors being equal, they grow larger in the presence of an abundant and regular supply of calcium carbonate, or in the warmer, normally salty seas of any given plane in time.

There is, in any event, a relationship between mode of life, size of breeding population, number of offspring, and individual survival prospects which is important to the paleobiogeographer. But survival of the individual is only one of the factors that controls survival of the species, and there is probably an optimum size to breeding populations which varies in the same direction as numbers of offspring and is related in some way to mutation incidence. The paleobiogeographical evidence, moreover, is seriously affected by the ability of a species to survive in the rocks as well as in time. Because of this, paleontologists concentrate on organisms with preservable hard parts, on special types of deposits where the imprints or remains of soft-bodied organisms may be preserved, and on sedimentological evidence that bears on the nature of burial and amount of movement after death.

Dispersal

The factors already discussed define the conditions of existence. Whether a given species, community, or biota actually exists at the various places where it might, if it could gain a foothold and displace competitors, depends also on its ability to be dispersed, on the migration routes available for dispersal, and on the barriers and natural filters that block dispersal or permit the passage only of particular biotic elements, in a particular direction, or by chance. This, in turn, depends in large degree on the global wind and water circulation, and on the geographic configuration of the earth, which varied in the past. The factors involved are well illustrated by the phenomenon of bipolarity (e.g., Wimpenny, 1941); by differences and similarities between the Recent and Tertiary marine faunas on opposite sides of the Isthmus of Panama, on which Woodring (1959) reported at this Congress (see also Woodring, 1954); by the now classic differences between the Tertiary mammalian faunas of North and South America (e.g., Simpson, 1953, pp. 21, 55); by recent Mediterranean faunal changes (Pérès and Picard, 1959); and by the well-known marsupial faunas of Australia and the success with which later introduced placental mammals were able to establish themselves there. Some of the variables are illustrated in Fig. 5, and others will be discussed.

The reproductive cycle is the internal control. All vertebrates and ovoviviparous invertebrates disperse by moving themselves, or by transport on other moving objects. Most marine invertebrates and plants, however, broadcast numbers of fertilized eggs, larvae, spores, or seeds which are carried about by currents, wind, or more esoteric mechanisms. High mortality is balanced by larger numbers of offspring (Fig. 4), and is reduced in some bottom-dwelling invertebrates by a limited ability of the individual larva to select its substrate (Thorson, 1946, pp. 463–466).

Other factors being equal, highest probabilities for dispersal are naturally enjoyed by species with large breeding populations that live at times of the maximum extent of favorable climatic and

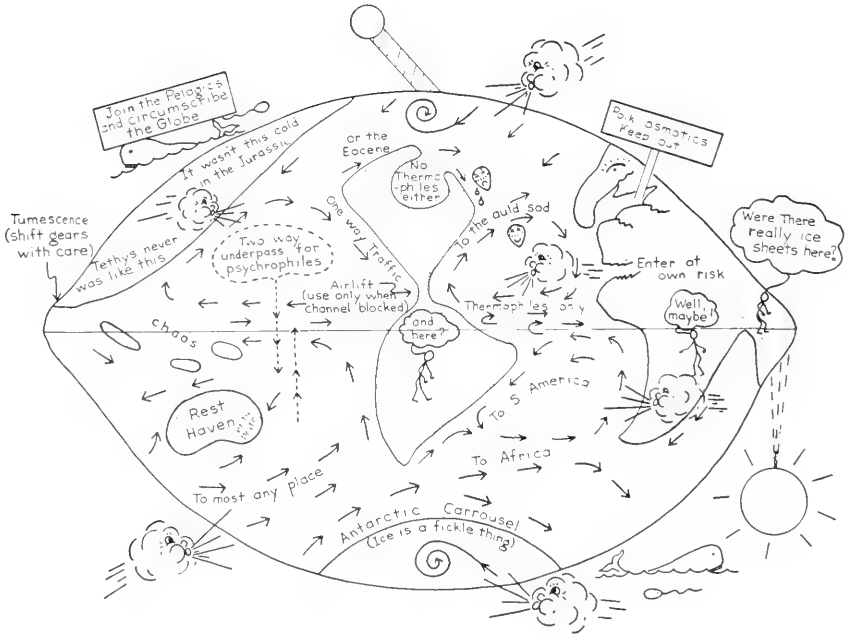

Fig. 5. Life at sea as the paleobiogeographer sees it and as it might have been.

ecologic conditions and optimum geography, as Axelrod (1952) showed for the terrestrial angiosperms. On the other hand, the more widely spaced the sites of habitable environment, the more ingenious are the devices through which the successful migrant attains dispersal. This is particularly true of certain euryhaline estuarine species which may go through resting stages like those of the nonmarine mollusks, during which they can be transported on floating objects or blown about by the wind; of the cold-water diatoms, whose resting spores may be carried across the inhospitable equatorial regions by way of the upper atmosphere; and of the polychaete annelids. The polychaetes, indeed, have the largest number of cosmopolitan species among the marine benthos (Thorson, 1950, pp. 30–33, 38; Cloud, 1959a, pp. 395–396) simply because those species, like some of the actinians and sponges, are able to undergo different forms of reproduction and larval development according to local conditions (Thorson, 1946, pp. 427–429, 476; 1950). Otherwise widespread living organisms, some narrowly restricted in their adult choice of habitable conditions, are characterized as a rule by easily dispersed, long-lasting early stages, and it is a proper working hypothesis to consider that the same was probably true in the past.

The most widely distributed types of marine organisms in modern times are as follows:

1. Actively nektonic organisms such as fish, cetaceans, and some cephalopods.
2. Planktonic organisms, and those which at some stage in their lives may attach themselves to, or be carried naturally within, members of the migrating nekton or floating objects such as driftwood or pumice. (The paleogeographer does not bother about ships except in choosing analogies, or before Jurassic time about birds.)
3. Brackish-water mollusks, plants, and insects characterized by viviparous or parthenogenetic reproduction; or by spores and resting stages which may be transported by wind (and birds), or on floating or swimming objects, and which may undergo long periods of estivation.
4. Organisms such as marine annelids which have great larval and reproductive lability.
5. Species of shallow, warm, or temperate marine waters with long-lasting planktonic larval stages.
6. Deep-water and cold-water species having abbreviated larval life or viviparous (including ovoviviparous) reproduction and able to move or drift with deep currents (Bruun, 1957, p. 663).

The paleobiogeographer should have good reason for eliminating the above categories, as well as the peculiarly geologic uncertainties and the statistical probability of viable freak transport, before concluding either that geographic factors require otherwise similar fossil populations to belong to nomenclaturally different species, or that drastic paleogeographic changes are in order.

Wind transport deserves emphasis beyond the mere notation that dispersal of spore-forming organisms can be so achieved.

Since the volume and weight of an object varies as the cube of its median diameter and the surface area only as the square, it is obvious that the likelihood of movement by wind increases with decrease in size, assuming similar specific gravity and, on the part of aquatic organisms, proximity to air-water boundary. As early as 1830, Ehrenberg described a variety of microorganisms from atmospheric dust, but Charles Lindbergh made the first *in situ* collections of high-altitude aerial plankton on his flight over the Greenland ice cap in 1933 (Meier, 1935). Gislén (1948, pp. 124–125) reports that it is common for animals up to a few millimeters long (especially fish) to be transported by winds, and he records aerial transport of animals as much as 10 cm long. If inferred prevailing or seasonal wind tracks fall in the right places and directions for the times involved, they could provide sweepstakes routes (Simpson, 1940a, pp. 152–157; 1953, pp. 23–25) whereby very rare but significant successful passages might account for the transport of exotic marine biotal elements that otherwise appear to demand the movement of established land barriers or the emplacement of temporary shoals across historic deeps.

With regard to the more orthodox forms of transport by water currents, various limiting factors are involved. Most important are the characteristic sites of adult and larval existence and the presence of tropisms with regard to light, current, or bottom; the direction, orientation, temperature, and depth of the current or passage along which movement may take place; and the nature and orientation of natural barriers and filters.

Planktonic eggs and larvae are more easily dispersed, but those that stay on or near the bottom are less likely to be eaten or to drift into unfavorable areas. The advantage varies according to the conditions and degree of continuity of tolerable adult and breeding habitat. The dispersal and persistence of species that inhabit warm and shallow waters is favored by larvae that drift near the surface in the mild equatorial currents, provided larval existence is not so long as to carry them beyond contiguous favorable bottom, or is long enough to ensure dispersal across surrounding deeps and near-continuous occupancy of more remote shoals. A similar degree of drifting for the stenothermal benthos of cold and deep waters presents greater hazard of introduction to inclement biogeographic realms. Natural selection, therefore, accounts for the abbreviated larval life or viviparity that characterizes cold-loving (psychrophilic) species and those of narrow depth range (stenobathyal). In the cold-temperate waters around Denmark, Thorson (1946, pp. 472–479) found that about one-third of the bottom invertebrates have a short or no pelagic life, whereas two-thirds have a larval life little exceeding three weeks on an average (longer in the same species in wintertime, presumably because of metabolic retardation). It would be interesting to have a similar study of the reproduction and larval development of warm water species. This should show lengths of planktonic larval life corresponding to the spacing of deeps and shoals, and degree of endemism.

Consider the implications of larval life and currents for dispersal. In an ordinary half-knot current a floating object could travel 170 km in a week or 500 km in three weeks; a two- to four-knot current like the Gulf Stream, if it were persistent, could travel 700 to 4000 km over the same time. Conceivably, therefore, a species with long-lived larvae and luck could cross the narrower parts of the Atlantic in one jump! If the larvae are attracted to light (phototropic) and currents (rheotactic), they are more likely to stay near the surface and in the main drift, and long larval life with a range of substrate selectivity (Thorson, 1946, p. 479) accordingly increases the possible distance of individual dispersal and the prospects of continued existence of the species, assuming favorable current patterns.

If, on the other hand, planktonic larvae or adults habitually live at depths greater than those of available transport channels, they can be moved through such channels only as a result of upwelling movements at the right time and place. Thus many pelagic microorganisms are rare in shallow-water deposits because they live suspended at some favored range of depth well below the surface, perhaps most commonly near the bottom of the photic zone where the phytoplankton have the first chance at upwelling mineral nutrients and the zooplankton the richest grazing grounds. An illustration of the possible paleobiogeographic significance of this is provided by the Tertiary Panamanian passage, which at times may have retarded the movement from Atlantic to Pacific (and the reverse) of deep-floating plankton, while facilitating the passage of near-surface plankton, including the pelagic larvae of benthonic species. The mere fact of a pelagic existence does not assure wide or instantaneous dispersal, nor does a benthonic adult life exclude geologically rapid and wide distribution.

Clearly, also, the intrinsic characteristics of migration routes and obstacles to migration are highly significant. Simpson (1940a, b, 1952, 1953), who has discussed this question philosophically, with special regard to terrestrial mammals, aptly describes the paths of interchange as corridors, filters, and sweepstakes routes. Most migration routes in the sea are to some degree filters. Currents provide easy downstream transport but retard upstream movement. East-west currents are likely to be temperature barriers to shelf and littoral biotas, and north-south currents, like the American limb of the Gulf Stream, may abandon the hapless larva (or adult) beyond the limits of its temperature tolerance or reproductive range. Passes between land areas or into epicontinental seas may be subject to fluctuations of salinity and turbidity that will exclude organisms sensitive to these variables.

Land masses that trend from north to south are likely to deflect currents into areas where they would not otherwise flow, as the north equatorial current of the Atlantic Ocean is turned northward under the influence of Coriolis force to become the Gulf Stream today. Sharp faunal distinction is common from eastern to western sides of such lands. Wide oceanic depths, like those of the eastern North Pacific, are barriers or sweepstakes routes to benthonic biotas in the absence of strong (steady or episodic) transverse surface currents. Given continued accretion of the hydrosphere (Rubey, 1952) or subsidence of ocean basins through geologic time, however, combined with long duration of present or antecedent oceanic rises, even transoceanic "bridges" become possible at some places and times (Axelrod, 1960, Figs. 6, 8, and 9). For the broadly cosmopolitan abyssal communities that cover half the globe (Bruun, 1957) and for the cold-loving bipolar benthos, the depths themselves are corridors beneath the equatorial surface waters and staging areas for invasions of the hadal depths (Bruun, 1957, pp. 654–661; Wolff, 1960).

Interpretive Basis of Marine Paleobiogeography

General Probabilities

Those familiar with the geographic distribution, sedimentary associations, and nature of the fossil marine biotas recognize that parallels can be drawn with the distribution of modern marine organisms. Some paleobiogeographic generalizations that appear to apply over a wide range or all of fossiliferous time are listed on Table I. With the exception of No. 14, these categories are not considered further. The citation of case histories would only document associations that follow from distribution characteristics already discussed, and I have reviewed the more specifically ecologic principles and methods elsewhere (Cloud, 1959b). It is of more interest in the present context to get on to subjects involving latitudinal zonation and orientation, for which a brief review of paleoclimatology is prerequisite.

Paleoclimatologic Essentials

Paleobiogeography, in fact, may be characterized as the mirror of paleoclimatology, in which the blemishes that make it interesting are due to geographic or physiographic (including geomorphologic, bathymetric, and substratal or faciological) isolation, the filtering properties of migration routes, and the intrinsic properties of biologic systems—giving rise to the provincial categories recognized by the Termiers (1957, 1959, pp. 81–98) and listed at the right side of Table I.

Climate itself depends on the circulation of the atmosphere (Fig. 6) and the sea (Fig. 5), the distribution of land and water, the position and inclination of the earth's rotational axis, the composition of the atmosphere, the path of the earth about the sun, and on strictly solar manifestations. Wexler (1957) has summarized modern concepts of atmospheric circulation; Trewartha (1954) has discussed the elements of modern climate; Landsberg (1958) has reviewed recent climatic trends; and Brooks (1949), Schwarzbach (1950), and Lasareff (1929) have suggested physical methods for deducing ancient climates. Shapley *et al.* (1953) have reviewed possible causes, effects, and evidences of

TABLE I. Some Recurrent Broad Categories of Marine Communities and Biotas, and Their General Paleobiogeographic Implications[a]

No.	Distribution	Variety	Special Systematic Features[b]	Endemism	Probable General Paleobiogeography	Termier Provinces
1	Wide	Small	Shells thin or absent, poikilosmotics present	Slight to moderate	Circumpolar or deep water	Climatologic or Physiographic
2	Local	Small and consistent	Shells thin or absent, poikilosmotics present	Marked	Isolated cold	Relict-Physiographic
3	Local	Small and consistent	Shells thin or absent, poikilosmotics rare or missing	Marked	Isolated hypersaline	Relict-Physiographic
4	Local	Small and sharply gradient	Thin shelled mollusks, fish, and crustaceans; poikilosmotics rare or missing	Marked	Estuarine	Relict-Physiographic
5	Wide	Large	Abundant calcareous shells	Slight to moderate	Temperate, shallow, and essentially continuous	Climatologic
6	Wide	Maximum	Abundant and commonly thick calcareous shells or tests	Slight to moderate	Warm, shallow, and essentially continuous	Climatologic
7	Wide	Large	Abundant and commonly thick calcareous shells or tests	Moderate	Warm, shallow, and discontinuous	Climatologic-Stepwise

8	Local	Moderate	Abundant and commonly thick calcareous shells or tests	Marked	Warm, shallow, and isolated	Relict-Physiographic
9	Wide	Moderate to large	Microscopic and non-calcareous, with filaments or floating devices	Slight	Circumglobal cold pelagic	Climatologic-Expansive
10	Wide	Moderate to small	Microscopic and calcareous with filaments or floating-devices	Slight	Circumglobal warm pelagic	Climatologic-Expansive
11	Wide	Small	Aquatic vertebrates	Very slight to none	Circumglobal to world-wide, nektonic	Expansive
12	Wide	Small	Aquatic angiosperms	Slight to marked	Shelf	Physiographic
13	Wide	Small	Dasycladacean or codiacean algae	Slight to moderate	Warm, photic	Climatologic-Physiographic
14	Wide	Small to moderate	Mainly tracks and burrows of regular pattern in flysch facies sediments	Broad similarity through time and space	Deep, infauna preponderant	Physiographic-Stepwise

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[a] Exclusive of many significant components of special and overlapping application such as corals and small benthonic Foraminifera.

[b] Invertebrate unless specified.

climatic change; and Rukhin (1957) and Durham (1959) have summarized paleoclimatic indicators and manifestations. The slender classic by Dubois (1895) is as nice an illustration as we have of the nature of the geologic evidence and reasoning, despite the 65 years that have elapsed since it was published. And, for the future, the way to more rigorous analysis of paleooceanographic data and reproduction of ancient marine currents has been outlined by Stommel (1957) and von Arx (1957).

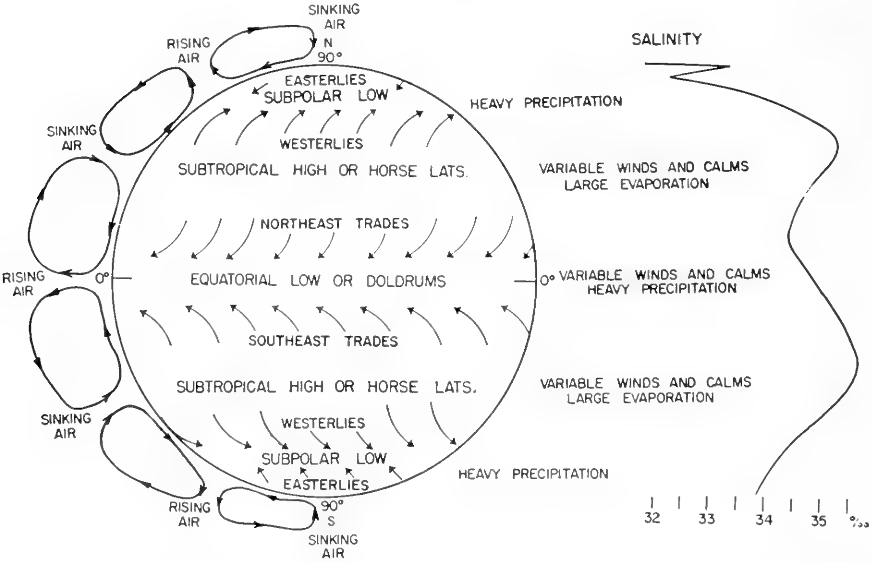

Fig. 6. Schematic tropospheric wind system for a hypothetical water-covered earth with strong latitudinal temperature gradient and mean annual salinities of present surface waters (slightly modified after Fleming in Hedgpeth, 1957, pp. 90–91).

From these and other works we know that the rotation and frictional effects of the earth, the position of the polar axis, the pull of the sun on the equatorial bulge, secular variations of the solar heat budget, and thermal variations of the atmosphere are responsible for the major wind fields—their location, orientation, breadth, and strength—and that wind patterns and size and orientation of land masses are the principal determinants of ocean currents. If, to these, we add the Coriolis deflection, the monsoon effect, the thermal influence on oceanic circulation, and the general relief and land connections, we have named the paleoclimatic and paleocurrent factors that can profitably be considered, and which give rise to the broad biogeographical subdivisions of land and sea, best reflected on a worldwide basis by the distribution of marine plankton (Fig. 7).

Employing a rotating tank apparatus similar to that of von Arx (1957) to create patterns of oceanic circulation for various paleogeographic models for the same time interval, and allowing for effects on the planetary wind and current system of secular variations in the latitudinal distribution of heat (Brooks, 1949, pp. 50–53), the paleobiogeographer could experimentally determine which circulation pattern best satisfies known biotal distributions and his climatic inferences. He can, of course, do the same thing with a crayon on a globe, or with pencil and paper, but in any case it is of value to check the dynamic details on experimental models. Such an approach could greatly improve the basis of paleoclimatology and more effectively test the relative probability of apparent polar wandering, continental drift, or stability of the outer crust and continents at various times in the past.

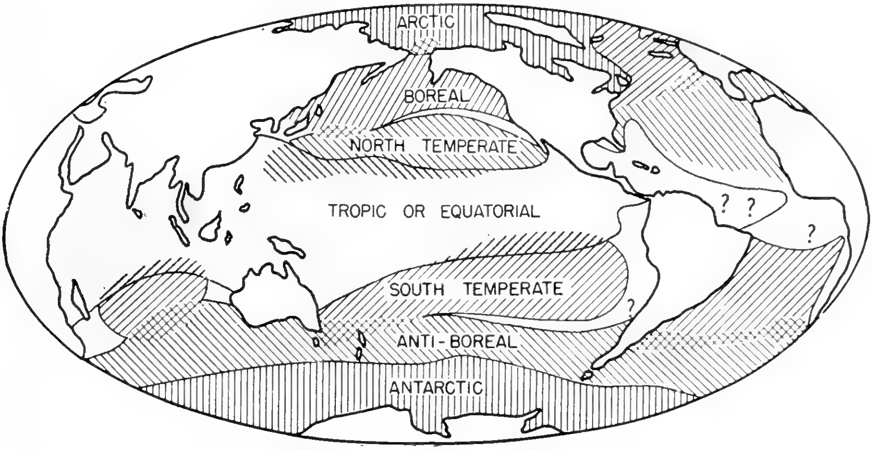

Fig. 7. Circumglobal biogeographical belts as defined by marine plankton (mainly according to Steuer, 1933, as modified by Hedgpeth, 1957, p. 367).

Identification of Equatorial and Polar Positions

Given a particular distribution at the present surface of the earth of reliably determined fossil organisms, communities, and biotas whose ecologic significance is believed understood, the special job of the paleobiogeographer is to relate these variables consistently. Factors complicating this task include the parallelism between the latitudinal and the vertical distribution of life, heat transport by water currents, parallel origins of similar associated phenomena, and the poleward migration and blending of paleobiogeographic temperature indicators at times of less-marked latitudinal temperature zonation.

Brooks (1949, pp. 50–53, 189, 192–197) illustrated the dependence of the present wind scheme on the pressure balance between poleward temperature decrease in the lower 8 km of the atmosphere (troposphere) and the poleward *increase* of temperature in the stratosphere. He discounts the significance of the glacial anticyclone per se. Lessening of the tropospheric temperature gradient poleward would reduce polar air pressures and result in repression of the polar easterlies and expansion poleward of the westerly wind systems and the low-latitude trade winds. The global system of ocean currents would necessarily undergo parallel changes, with the result that all their boundaries would be moved poleward (Figs. 5–7) and eventually eliminate the easterly polar currents. This would accelerate the warming effect at the poles and further reduce the actual temperature gradient between poles and equator, as (Dubois, 1895, pp. 72–99) would also be the case in the event of greater general input of solar heat.

The accepted technique for the paleobiogeographical location of equator and poles for a given time interval is to draw a line through the middle of an areal distribution pattern of biological indicators of warm water, and then to find the locus of points that would have been about 90 degrees from such a line by moving poles or continents until the best fit is found. If the paleobiogeographer is to contribute critically to hypotheses of polar migration and continental drift, he should also be constantly on the lookout for the most reasonable interpretations of his evidence in the light of climatologic and ecologic variables, without too much regard for what anyone else thinks may have happened to the crust, but with a healthy awareness of its physical properties.

It is, of course, important not only to arrive at correct conclusions, but to do so for the right reasons—to analyze in terms of processes, energy relations, reaction rates (intensity and time), phases, and components, and not merely of empirical analogy. For example, abundance of calcium carbonate (as coral and other organic reefs, as beds of thick-shelled mollusks and Foraminifera, or simply as limestones and dolomites without regard to skeletal composition) is commonly interpreted as evidence of former tropical conditions. Such abundance of itself does not demand any specific temperature conditions or latitudinal restriction. Rather it demands persistent saturation, which can happen at any temperature or latitude if enough calcium and carbonate ions are present in proportion to other ions in the solution. Because temperature is an important factor with regard to the carbonate ion, other factors being equal, the prospects of calcium carbonate precipitation *will* increase with increasing temperature. No matter how cold or warm the oceans were at any particular time, however, they can hold only a finite number of calcium (or magnesium) and carbonate ions before precipitation begins. Thus, assuming the generally constant composition of sea water, the proportion of carbonate sediments and shells at any given time should vary with latitudinal or local temperature, and the total amount of calcium carbonate precipitated should be a general function of world climate. The general interpretation, it seems, is probably justified, but not for the reasons usually given; and the reasons are important because their misapprehension can lead to unwarranted narrowing of objective alternatives. Thus, an abundance of either organic or inorganic calcium carbonate of great age at currently high latitudes may mean, for the time of deposition, either a greater general uniformity of climate, the deflection of warm currents poleward as a result of special terrestrial configuration, a preceding climatic shift from *relatively* cooler to *relatively* warmer, changes in carbon dioxide tension or ionic composition of the sea, or shifting of the poles or crust. Here also Brooks (1949, pp. 133, 150–151, 204, 206;

1951, p. 1017) has provided useful reference data in the form of paleotemperature equations, as well as his own estimated and calculated mean temperatures for various intervals from the Pre-Cambrian onward—computations soon to be outmoded, we may hope, by isotopic paleotemperature data.

Although the subject is not exactly marine or biogeographic, physical evidence taken as indicative of pre-Pleistocene ice sheets is also fundamental to the problem of polar location. This is too important to be left to the experts and too prevalent at low latitudes to be accepted as representing latitudinal changes without seeking other explanations both for the deposits and for how those demonstrably glacial came to be so. Crowell (1957) has aptly underscored the similarities between tillites and pebbly mudstones due to other forms of gravity mass movement, specifically marine, and the point needs no repetition to one who has seen both. Even striated pavements are not sacred; they also can be produced by other and more rapid gravity movements than the creep of frozen water (e.g., rock or gravel slides, nuées ardentes). Paleoglacial events that survive the called-for critical reexamination and are too big to be the product of mountain glaciers may still be explained by the same adiabatic cooling of rising moist winds that explains the mountain glaciers, but on a larger scale, as Brooks (1949, pp. 252–257) suggested may be the case for inferred Gondwana glaciation.

Finally, we have to consider an ingenious and purely biologic scheme elaborated by Ma (1952, and series of papers there cited) for determining paleolatitudes on the basis of interrupted growth in corals, and his interpretations in support of theories invoking a blend of polar and crustal drift. Ma's data themselves, however, are open to other interpretations. The formation of growth zones in a coral (or a mollusk) are a function of metabolic variations that could be and probably are related to a number of environmental factors other than temperature. They are not really comparable, for instance, to those of deciduous woods, which annually pass through a temperature-controlled interval during which growth can proceed only from already stored nutrients, an effect that overshadows all other growth variations of the individual tree.

Samples and Problems from Marine Paleobiogeographic Record

In the immense ranges of geologic time it is inevitable not only that a great range of individual paleobiogeographic patterns should occur but also that certain broadly overriding combinations will repeat themselves. The most familiar of these overriding patterns to the marine paleobiogeographer are the Tethyan and Antarctic transport routes and the Panamanian and Gondwana barriers (or filters).

By way of illustrating both that reasonable biogeographic interpretations can be made over a wide range of past time and that great problems remain unsolved, a few lines will now be devoted to these and other reconstructions from different parts of the geologic record.

Early Cambrian Biotal Provinces

Near the dawn of recognized metazoan life, in the opening scenes of the Paleozoic era, an expansive paleobiogeographic realm is represented by the broad-headed olenellid trilobites (Order Redlichiida) of Early Cambrian and earliest Middle Cambrian age, with three provinces defined by distinctive genera or generic groups. Figure 8 illustrates the known global distribution of these provinces, compiled by the Termiers from the labors of generations of Cambrian specialists. Although the distinctive "genera" are now sometimes finely subdivided, and are not strictly contemporaneous (Öpik, 1958), their paleobiogeographic distinction is a fact. In a general way *Olenellus* represents a North American province, *Redlichia* a combined Tethyan and Cathaysian province, and *Holmia* a North Eurasiatic province. The generic names are simply by-names for the larger faunal (mainly trilobitan) assemblages they characterize, like Petersen's communities and d'Orbigny's zones. These assemblages are primarily associated with argillaceous detrital deposits near the continental margins of their time; and, as for the olenellids themselves, their broad, flat shapes, their inability to enroll in adult stages, and the tracks they have left in the sediments suggest that they were members of a mud-grubbing benthonic fauna whose early broad differentiation into endemic genera and faunal provinces reflects the gradual

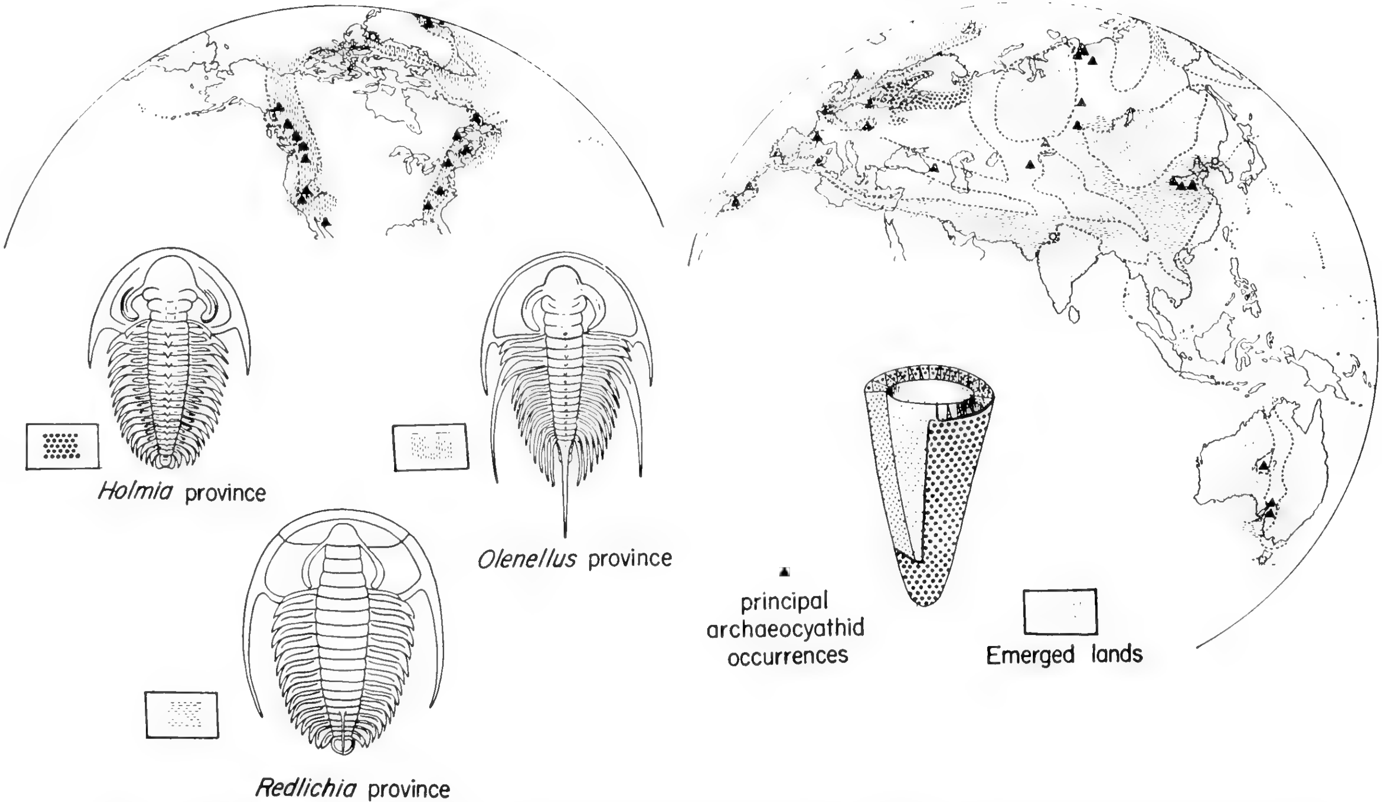

Fig. 8. Marine paleobiogeographic provinces of the Early Cambrian (modified after Termier and Termier, 1959, pp. 28–29).

dispersal through relatively brief larval stages more than it does provincial environmental differences.

In the photic zone of the shelf and bank seas adjacent to or within these olenellid provinces, calcareous spongelike archaeocyathids joined with a variety of lime-fixing algae to create reef-like organic buildups from the mouth of the Khatanga River in Siberia to central East Greenland and to the Beardmore Glacier area of Antarctica. The presence of a variety of filamentous and botryoidal algal structures associated with the archaeocyathids confirms their preference for the shallower and probably warmer parts of the Cambrian seas.

Conversely, the detrital and weakly calcareous deposits of the adjacent olenellid assemblages imply deeper, cooler waters for them, which is consistent with the generally modest endemism and smaller biotal variety of the olenellid provinces. Moreover, although the archaeocyathids were locally able to establish themselves in the shallower parts of the olenellid provinces, the olenellids were seemingly not able to migrate across the broad epicontinental reaches of the shallower and more extensive archaeocyathid seas, as in Siberia. Around the central core of North America the olenellids generally occur inside the belt of archaeocyathids, which may mean either that the latter occupied narrow shelf seas adjacent to offshore lands and defining the outer edge of geosynclinal olenellid seas, or that deeper shelf seas with olenellids were separated by shelf-edge archaeocyathid reefs from the yet unknown geosyncline proper further offshore. More evidence is needed to resolve this problem.

Regardless of its more specific details, the described fourfold biogeographic classification of the Early Cambrian biotas is fairly interpreted as implying a regional sedimentological and bathymetric subdivision within a generally warm global climate of little, or yet undeciphered, latitudinal variation. Information so far synthesized neither demands nor opposes a different latitudinal orientation from the present one.

Gondwana

Intermittently from middle Paleozoic (Devonian) through at least early Mesozoic (Triassic) time, significant fractions of the marine and terrestrial biotas of the southern hemisphere were enabled to encircle it, but were retarded as to movement in a northward direction, or receipt of northern admixtures, by something geologists like to call Gondwana [Land of the Gonds (Caster, 1952, p. 126)]. Gondwana, or Gondwanaland, has commonly been interpreted as a more or less east-west, transoceanic land mass whose composition varies with author and time but which generally includes a large part of Africa, usually parts or all of South America and India, and commonly Australia and Antarctica (for recent summaries see Teichert, 1958; King, 1958).

Similarities in the Early Devonian marine faunas of South America and South Africa have long attracted attention, and recently have been extended to include Tasmania (Boucot and Gill, 1956). These similarities played a prominent part in a recent symposium on the problem of land connections across the South Atlantic (Mayr *et al.*, 1952) and were one of the key factors leading to the principal conclusion drawn by some participants of that symposium that a "faunal connection" and presumably a land connection "seems to have existed until at least 180 million years ago, but was no longer in existence 130 million years ago" (Mayr, 1952, p. 257). Indeed, the evidence for continuity of Devonian land between Africa and South America was so vigorously and persuasively presented by Caster (1952) as to stimulate review and search for an alternative.

Figure 9 compares Early Devonian faunal relations from South Africa to South America, with different patterns of distribution found among the living shelly benthos and an Oligocene Tethyan example. These data, to be sure, are of very unequal value, and some are badly in need of revision and refinement. They do, however, give a rough order of relations which may be interpreted as implying either (1) a similarity of biogeographic relations between the southern hemisphere marine Devonian and the Oligocene Tethyan and Recent Indopacific, or (2) a tendency toward a higher proportion of nomenclatural identities between contemporaneous smaller faunas of like ecology regardless of other factors.

I am not merely quibbling, therefore, when I urge, as Dunbar

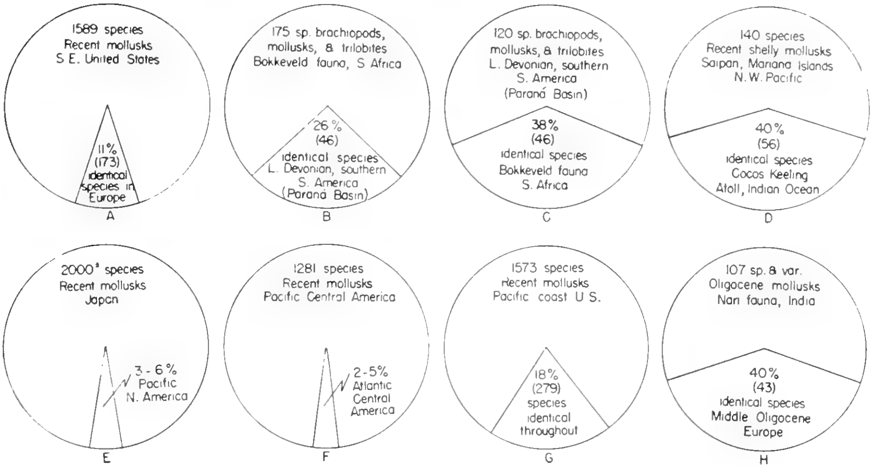

Fig. 9. Nomenclatural identities among described shelly marine benthos in Early Devonian of Southern Hemisphere compared with different patterns of distribution among the living shelly benthos and an Oligocene Tethyan pattern. A (Dall, 1889; Durham, 1952) and E (Keen, 1937; Durham, 1952), transoceanic, subtropical to temperate; B and C (Caster, 1952, pp. 114–116), Devonian, in question; D (Cloud, 1959a, p. 395), transoceanic, tropical with island stepping stones; F (Durham, 1952), across north-south isthmian barrier, tropical; G (Durham, 1952), north-south shoreline, temperate; H (Durham, 1952), middle Cenozoic (Oligocene) east-west Tethyan shoreline.

(1952) urged, that other factors be considered in interpreting the impressive degree of nomenclatural identity between southern hemisphere Devonian marine faunas. Not only are the described faunas small but also, being from similar Paleozoic rocks and relatively inactive areas paleontologically, they are likely to be conservatively identified and biased in the direction of the more conspicuous, more readily identifiable species, and the brachiopods. Perhaps more nearly comparable data would be obtained if, for instance, among the modern Indopacific faunas one were to identify only the cypraeids and cones. The identities from Saipan to Cocos-Keeling (Fig. 9D) would then rise to from 40% to 70%, across more than 3000 miles of ocean and three opposing east-west current systems—a degree of similarity fully as remarkable as that of the southern hemisphere Devonian, even allowing for the shoal-water stepping stones between.

Assuming no crustal drift or foundering, we might expect to find analogies between the Devonian couple and the Recent North Atlantic faunas, which involve distances and potential intermediate stepping stones of about the same order of magnitude. Although such a comparison is hindered by the fact that mainly subtropical west Atlantic species are compared with temperate east Atlantic species (Fig. 9A), it is nevertheless impressive to find an 11% transoceanic nomenclatural identity between faunas of about 1600 species from different latitudinal zones. The same check list (Dall, 1889), incidentally, shows 6 out of 21 morphological species and varieties of living brachiopods native to the southeastern United States as occurring in Europe: a 29% identity that compares more favorably with that between members of the Devonian couple (Fig. 9B, C),

If, as it seems, similarities in the Early Devonian faunas of the southern hemisphere are not a compelling argument for former continental connection, how else may they be explained? These similarities could be explained without catastrophic geographic changes if eastward and northeastward flowing currents such as now encircle Antarctica as the great West Wind Drift (Fig. 5) existed in Devonian time and dispersed floating larvae from a circum-Antarctic shelf-sea to the shores of southern hemisphere land masses having similar marine faunas, and provided that such dispersal were repeated at frequent enough intervals to retard local endemism. That Devonian Antarctica was ice-free is implied by the presence of Late Devonian fish well up in the thick and apparently uninterrupted later Paleozoic terrestrial deposits of eastern Antarctica (Adie, 1952), and by the occurrence in the American sector of Early Devonian brachiopods which came to my attention through the courtesy of W. E. Long. The probable intermittent presence of isthmian linkage between Antarctica and other southern hemisphere lands (e.g., Axelrod, 1960, Figs. 6, 8, and 9) provides a contributary or alternative explanation, but probably it is not necessary to explain the paleobiogeographical facts.

The answer may be found in more and larger collections of Antarctic and other southern hemisphere fossils, which should be a primary objective of "Post-Geophysical Year" investigations.

Meanwhile available evidence for the Devonian seems at least as well explained by mechanisms that do not demand the former existence of a cratonic link or links as by those that do (see also Gill, 1958, p. 115).

But what of other evidence for Gondwana? The late Paleozoic *Glossopteris-Gangamopteris* flora, which Gondwana was invented to explain in the first place (Teichert, 1958, p. 563), has lost ground as proof of continental linkage with the discovery of associated winged sporelike bodies in the Permian of India, Australia, Antarctica, and perhaps South Africa (Virkki, 1937; Sahni, 1938, pp. 14–15, 20–21). Simpson (1953, pp. 61–62) concluded, "All the biogeographic features in the known history of mammals are best accounted for on the theory that the continents have had their present identities and positions." The fresh water galaxid fishes of southern South America, Africa, Australia, and New Zealand are widely euryhaline, and Myers (1949) suggested that they could probably cross the present ocean basins. Teichert (1958) finds present paleobiogeographic evidence to indicate the existence of open ocean west of Australia since early Paleozoic and isolation of Australia since Permian or earlier.

Gondwana as a transoceanic land mass, therefore, remains an as yet unsatisfactorily documented and biogeographically unnecessary hypothesis. Insofar as its biogeographic basis is concerned, the linking elements could just as well have been dispersed from an ice-free Antarctic center under the influence of the circum-Antarctic West Wind Drift or the wind itself, aided by the northward deflection resulting from Coriolis force; or, in the case of the terrestrial vertebrates, through demonstrable northern hemisphere routes.

The Gondwana glaciers are another problem (see King, 1958, for a recent viewpoint). If there were large waxing and waning ice masses anywhere during the right parts of the late Paleozoic, they might help to explain the extensive cyclothemic sedimentation of these times, repeating a regular succession of small rises and falls of the sea (or the land). However, as suggested earlier, the evidence for all supposed examples of pre-Pleistocene glaciation needs review in the field.

Tethys and Other Mesozoic Seaways

Repeatedly, from the beginning of latest Paleozoic time, the thick-shelled benthos and nekton of the world ocean encircled it over a route through the present Mediterranean depression and Middle Eastern and central Indian lowlands, except as hindered by transverse obstacles, mainly in the region of Central America. This meridional seaway is called Tethys, and it would function anew with moderate rise of the sea or subsidence of the land.

Tethys reached its peak after an interval of temporary blockage coincident with the dessication transitional from Paleozoic to Mesozoic times. The rich warm-water shelly faunas and reef biotas of later Mesozoic time spread from India to western North America (e.g., Smith, 1910, p. 482) and reached northward along more temporary routes to high latitudes, and even beyond the Arctic and Antarctic circles. Dasycladacean algae, denoting warm water in the upper photic zone, are common associates of some faunal facies.

The Jurassic (middle Mesozoic) has the best-documented record of the systems with intimate Tethyan connections. Uhlig (1911) showed that Neumayr's (1883, 1885) pioneer efforts toward a worldwide zonation of the Jurassic marine faunas were based on faulty analogy, but he sustained the idea of broad latitudinal zonation parallel to the present one. He extended the warm and temperate climatic zones northward and dispensed with Neumayr's cold zones. He also recognized nine separate marine provinces in the Jurassic, all with channels to the Tethyan seaway. Uhlig's scheme in turn has undergone revision by Arkell (1956, pp. 606–618), who reduced the provinces to three, Tethyan, Pacific, and Boreal. On the basis of his master work on the Jurassic geology of the world, Arkell concluded that the Early Jurassic (Lias) fauna was essentially universal and Tethyan; the divisions evolved later, with much shifting of boundary zones. Limestone is rare or lacking in high latitudes, but a conspicuously shelly fauna is recognized as far north as Greenland. Arkell (1956, p. 616) logically concludes that even the subpolar waters of Liassic time "were at least as warm as those of the present temperate zone." From the distributional data it would have been pardonable to call them temperate without qualification.

General Cretaceous (late Mesozoic) paleoclimatology runs in much the same vein as that of the Late Jurassic. The very widespread Cretaceous deposits and rich shelly faunas, however, offer enticing prospects of doing something more refined about the paleobiogeography. In the hope of spurring more interest in this, I have tried reconstructing a current system for the well-documented early Late Cretaceous seaway through North America (Fig. 10), connecting with the Tethyan seaway at the south.

The evidence of the ammonites and inoceramids from Greenland and northern Alaska (Imlay and Reeside, 1954, pp. 226, 242, and references there cited) and of the rich Cretaceous flora of west Greenland (Dubois, 1895, p. 13) confirms the warm-temperate nature of the Turonian climate of present Arctic regions. Hence (assuming no latitudinal change, and for reasons given) we may eliminate the polar easterly winds as an effective force and introduce a preponderant eastward current drift at high latitudes, driven by the west winds of a subpolar whirl. Such a current, presumably, would enter the northern end of the Rocky Mountain geosyncline, turn right under the influence of Coriolis force, and execute a clockwise gyral. Opposing this at the south, would be another clockwise gyral introduced by the Tethyan trade wind drift from the southeast in a similar way. Of course, numerous local irregularities would develop, but the two principal gyrals should impinge obliquely about at the present international boundary, and broadly separate different faunal provinces. The fact that the Turonian faunas of northern Alaska have Atlantic aspects (W. A. Cobban, oral communication) is not at odds with this. It is to be expected that entrainment of southern waters along the western side of the northern gyral, or even a narrow long-shore current from the south would filter some southern elements northward, and that the reverse might happen along the eastern side. There should, moreover, be a general coincidence of pelagic and shallow benthonic differences with the two suggested gyrals,

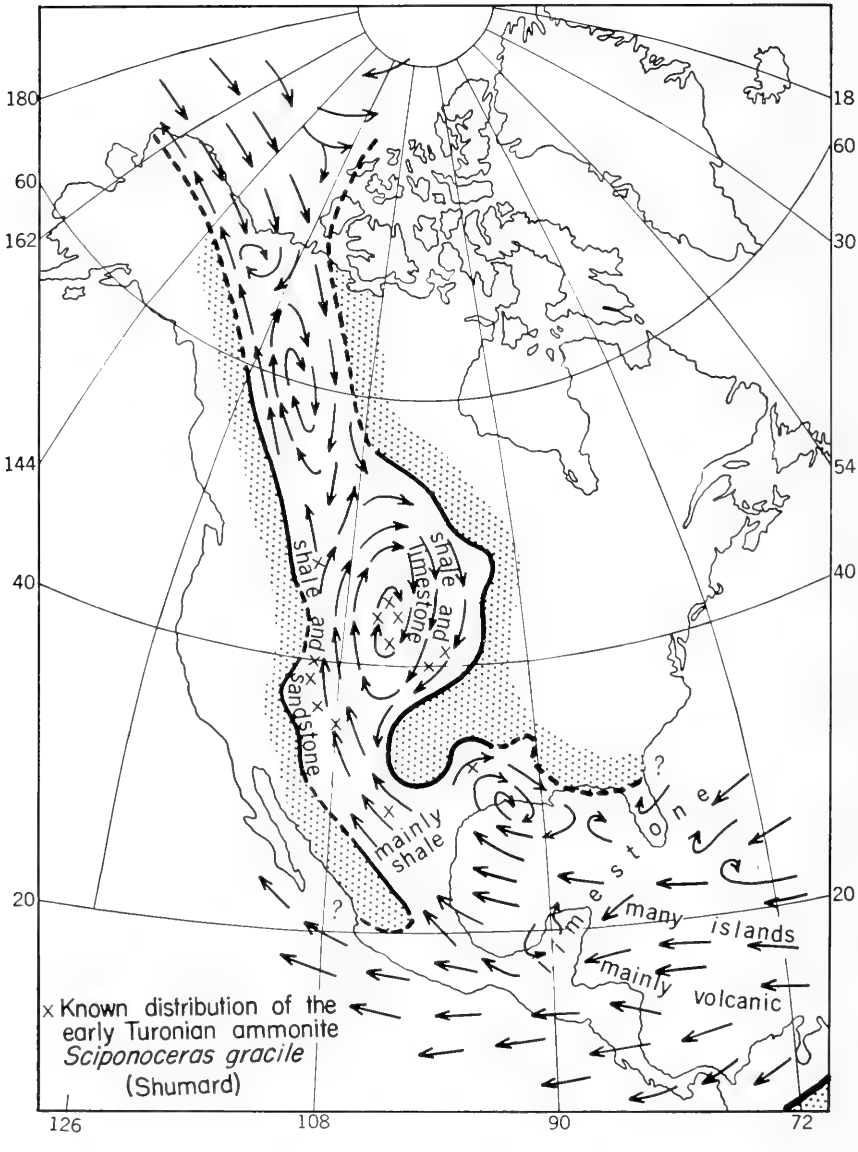

Fig. 10. Early Late Crustaceous (Turonian) seaway through Rocky Mountain geosyncline with inferred current patterns assuming no latitudinal change (shorelines adapted from Schuchert, 1955, map 73, and Woodring, 1954, Fig. 1).

as is hinted by the known distribution of the Turonian guide ammonite *Scipionoceras gracile* (Shumard), supplied by W. A. Cobban after the current system suggested in Fig. 10 was plotted.

It would be of interest also to analyze the history of the Panamanian link and its effect on current movement and evaporite-carbonate sequences of the northern Gulf Coast over a range of Cretaceous time, but that is another job.

A Passing Reference to the Tertiary

The Tertiary is replete with paleobiogeographical data of such a variety and degree of refinement as to offer a surfeit of choices for analysis. This has advantages and disadvantages, but the Tertiary has given us our best paleobiogeographic reconstructions of any antiquity, and Tertiary and younger Cenozoic relationships received much attention in the seminars of this Congress. Tertiary paleoclimates have been reviewed by MacGinitie (1958) and selected evidence from the marine realm bearing on Tertiary latitudinal zonation and progressive climatic deterioration has been condensed in papers by Durham (1950, 1952, 1959).

I could not bear to pass the Tertiary treasure box without at least mentioning the magnificent works of Ostwald Heer (1868–1883) and of Reid and Chandler (1933) on the older Tertiary angiosperms. Even though they are not marine paleobiogeography (and Heer's Arctic "tropical Miocene" is warm-temperate to subtropical Eocene and Paleocene) they establish the basis for paleoclimatologic conclusions that profoundly affect the marine realm. The already cited paleobiogeographic classic by Davis and Elliott (1957) on the London clay sea makes ample use of this data.

Flysch Facies

The flysch facies, a generally early syntectonic basinal sediment characterized by intercalated coarse redeposited clastics and fine-grained pelagic sediments, is the special topic at this Congress of Ksiazkiewicz (1959), who has devoted a large part of his productive life to it, and who undoubtedly knows more about more phases of the problem than anyone else here (e.g., Ksiazkiewicz, 1958). Nevertheless, because it is a subject of timely and growing interest, I venture to add my own interpretation of the flysch facies as representing a recurrent or time-transgressive paleobiogeographic realm of major significance.*

It is well known that aside from redeposited shelf assemblages, occasional pelagic species, and the rare occurrence of unusual and impoverished benthonic associations, the flysch biota is represented almost exclusively by a relatively small variety of tracks and feeding burrows of unusual regularity and distinctive form (e.g., Seilacher, 1954, Fig. 2; Cloud, 1959b, Fig. 6). Two things besides their regularity stand out about these *Lebensspüren* or trace fossils. First, they are pretty much the same all over the world and from middle Paleozoic, or earlier, to late Cenozoic. Second, they commonly cut across physical markings made by gravity emplaced sediments that were moved rapidly across and dumped upon the surface on which the organic markings were made later.

We know, therefore, that the mobile benthonic fauna responsible for the distinctive organic trackways and burrows of the flysch facies lived largely within the sediments—that it was primarily an *infauna*. It is evident, too, although we have never knowingly observed the makers of these particular markings, that the organisms responsible for them maintained or adopted broadly similar distinctive habits of feeding and movement, did not vary widely in size, and had functionally similar locomotor, digging, and feeding equipment through a remarkably wide range of space and time, and despite the relative geographic isolation of many flysch basins. If we assume that the animals as well as the tracks were similar, we have in effect drawn a very close parallel between the fauna of the flysch facies and the modern infauna of the cold aphotic depths as described by Thorson (1957, pp. 463–466) and indicated in Fig. 3. Even those species which worked at the

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* For purposes of this discussion I adopt an objective definition of flysch facies which demands that the coarse layers possess four critical descriptive features suggested to me by Prof. Ksiazkiewicz: (1) pronounced lateral continuity; (2) sharp bottom contacts and commonly gradational tops; (3) generally well-defined internal structure; (4) plentiful sole markings showing directional characteristics. It is only fair to remark that Professor Ksiazkiewicz does not himself insist on so restrictive a definition.

For further discussion of the problem see also R. Trümpy (*Bull. Geol. Soc. Am.*, *71* (6), 873–880 (1960) or the comprehensive monograph of N. B. Vassoevich, *The Flysch and the Methods of Its Study* (in Russian), Gostoptekhizdat, Leningrad, 1948.

sediment-water interface of the flysch seas commonly produced a regular pattern of searching and feeding tracks in the manner of many organisms that work in darkness, and some of the deep-sea photographs shown by the Soviet delegates to this Congress showed remarkably flyschlike organic markings.

I have previously approached this conclusion with more reservation (Cloud, 1959b, p. 944) simply because there has been so widespread a trend, uncritically following Ph. H. Kuenen's inspired lead and on what I consider less satisfactory evidence, to interpret all flyschlike sediments as deep-water deposits and too wide a range of sediments as flysch. However, the evidence so briefly reviewed above does strongly suggest that the known benthonic megafauna of the flysch facies as here defined represents an infauna of relatively deep water: probably mainly bathyal (below 200 m) and perhaps locally even abyssal. Evaluation of the microfaunal assemblages of the younger flysch facies deposits earlier led Ksiazkiewicz (1958, p. 419) and before him Grzybowski (Ksiazkiewicz, 1956, p. 387) to a similar induction. As defined by the markings left by its benthonic megafauna, moreover, the flysch facies can be considered to represent the farthest ranged and longest lasting paleobiogeographic realm (if it may be so called) in the recorded history of the earth. This, to be sure, opposes both the dictum that little is represented in the fossil record beyond shelf elements, and the suggestion sometimes made that the existing deep-sea fauna has evolved in younger geologic times from invasion of basins that were stagnant through a preceding epoch of little climatic differentiation. The idea of general deep-sea stagnation in the nonglacial geologic past is opposed not only by the probable persistence of a long-ranged flysch facies fauna but also by the antiquity of deep-sea elements such as the Monoplacophora, by hadal endemism in general (Wolff, 1960, pp. 100–102, 104), by the importance of oxygen-bearing turbidity current sedimentation and oxidized sediments in the deep sea basins, and by the certainty that there always was some temperature gradient between equator and poles and some frictional turnover of the water masses related to the opposing wind systems which must exist in order to maintain the circulatory balance of the atmosphere.

The rarity or absence of recognized contiguous shelf facies and intermediate equivalents is a principal difficulty with acceptance of the flysch facies as everywhere deep. Obviously there were contiguous shallow waters, and, although it is a stock suggestion that the flysch facies sediments have invariably been disconnected during compressive deformation, it seems certain that some of the equivocal flyschlike sediments will prove to be of an intermediate nature. A comprehensive survey of an undeformed flysch basin is badly needed.

Polar and Crustal Drift

To the paleobiogeographer polar wandering, continental drift, or slippage of the earth's outer shell are simply ways of changing the climatic zonation or of compressing or expanding biotic gradients. His concern with such matters is whether or not the paleobiogeographic evidence demands, is helped by, or is consistent with such movements; and, if so, in what direction and to what extent.

To apply Occam's razor to the problem, he should first consider whether observed distributions can be satisfactorily explained in the present framework of the earth, then explore other possibilities. I have done this elsewhere (Cloud, 1959b, pp. 946–948), although in far less detail and range than is needed, and concluded that the distribution of certain Paleozoic warm-water indicators could be explained about equally well with the equator where it now is, *or* through the poles.

The concept of great polar (and equatorial) drift, however, has been advocated on the basis of paleomagnetic data from the turn of the century onward (e.g., Kreichgauer, 1902). A recent variation (Fig. 11) is that of Runcorn (1959) and others, whereby concurrent continental and polar drift is called upon to explain separate paths of polar migration deduced from the data of remanent magnetism on different continents.

This is not the time or the place either to review the subject exhaustively or to ignore it wholly.* I will conclude, therefore, by

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* An excellent recent review is that of Allan Cox and R. R. Doell, Review of paleomagnetism. *Geol. Soc. Am. Bull.*, *71* (6), 645–768 (1960).

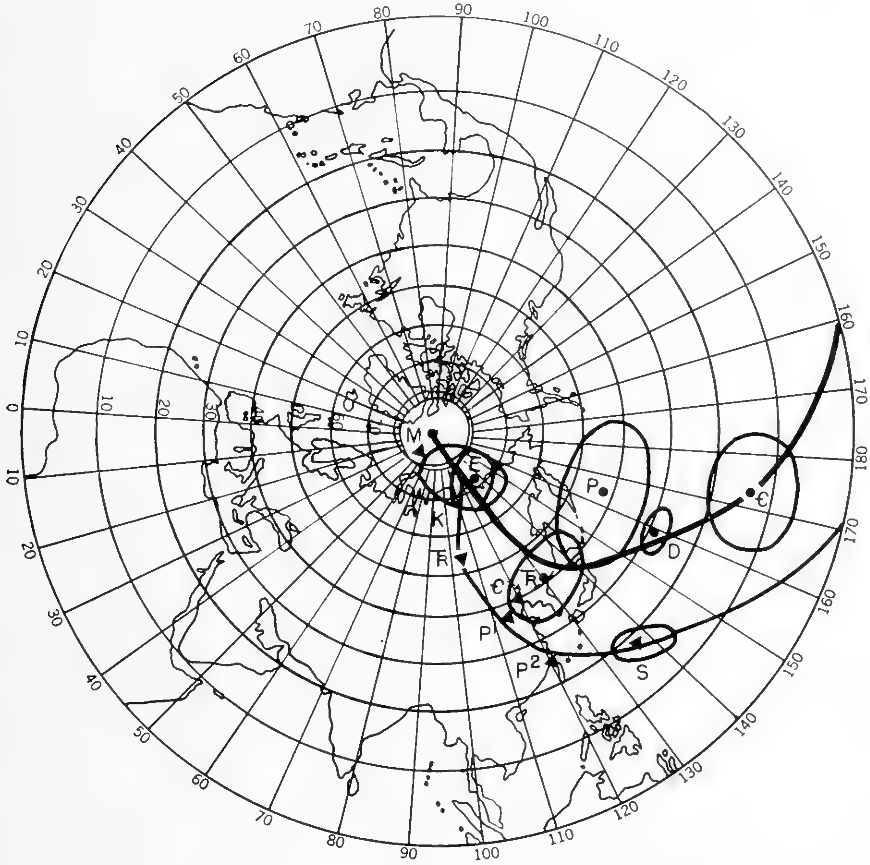
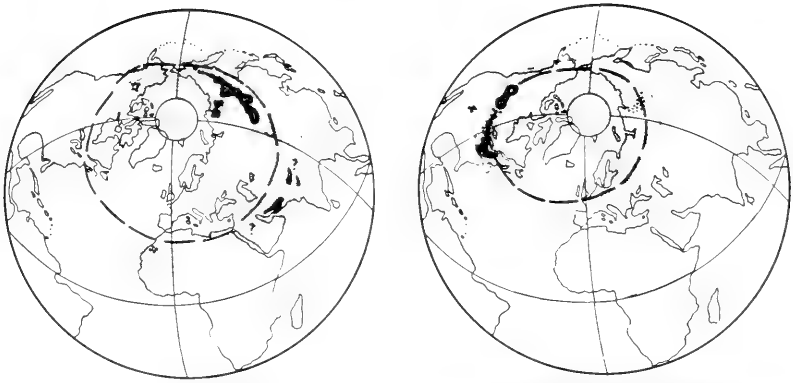


Fig. 11. Paleomagnetic polar positions and paths in the Northern Hemisphere according to Runcorn (1959, Fig. 5).

repeating Lotze's (1957) data on the Northern Hemisphere distribution of evaporites (Fig. 12). Contrary to Runcorn (1959, p. 1011), such sediments are not indicative of equatorial proximity, but of an accelerated rate of evaporation, commonly best developed in the zone of variable winds and calms between the trade winds and the prevailing westerlies (Fig. 6). The remarkable thing about Lotze's data is that from the Permian onward they conform nicely with the concept of a higher position for this zonal relation during the warmer climatic intervals when the polar easterlies were probably absent and the other wind belts wider. The pre-Permian



Cambrian Ordovician-Silurian

Permian Triassic

Older Tertiary Younger Tertiary

Fig. 12. (*Continued on facing page.*)

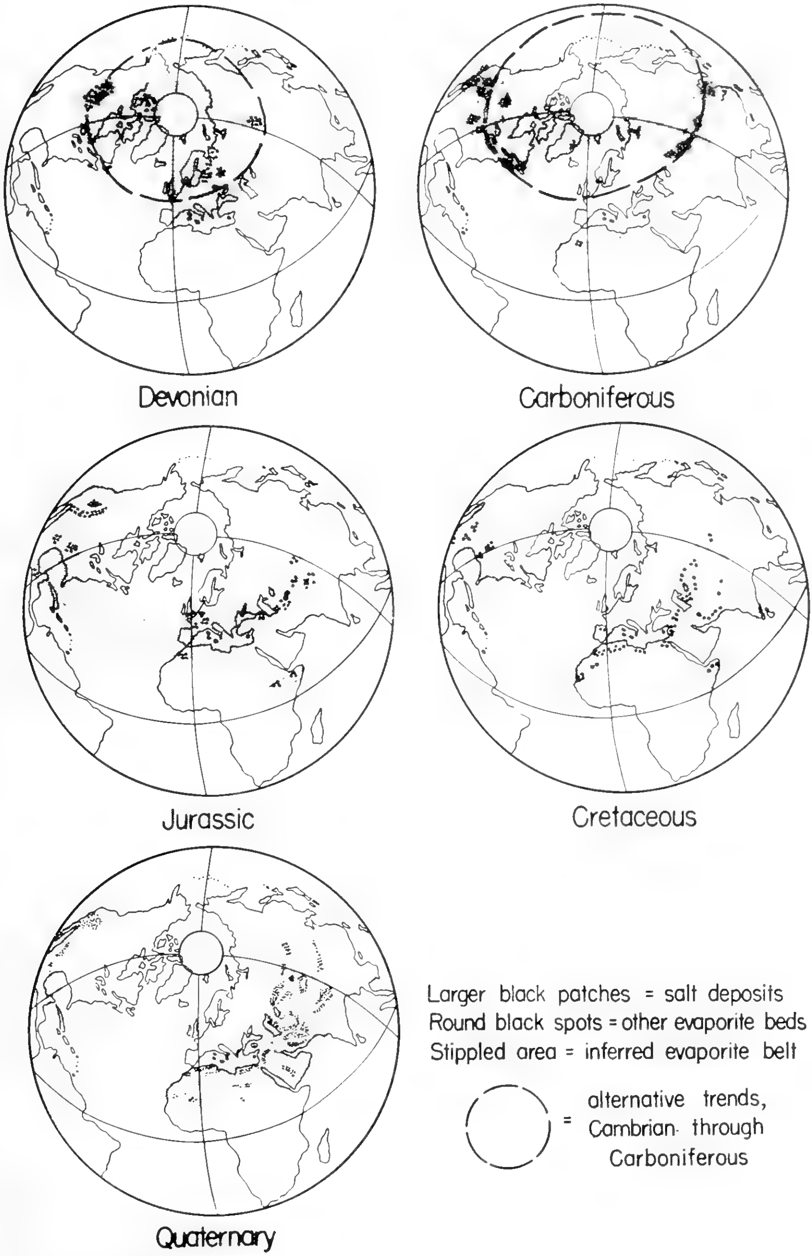


Fig. 12. Distribution of evaporites in the Northern Hemisphere for the geologic periods since the Pre-Cambrian (rearranged and slightly modified after Lotze, 1957, pp. 192–193, Figs. 77–86).

salt distribution is not distinctly zonal, and Lotze, who interpreted the data differently, connected his evaporite belts across the polar regions. I have taken the liberty of supplying alternative trends for these intervals, which I find not inconsistent with the idea of unusually moderate climatic conditions and very wide trade wind belts.

The evaporite patterns as I interpret them, therefore, reenforce the paleobiogeographical evidence favoring no post-Triassic and probably no post-Carboniferous drift (Cloud, 1959b, pp. 948–949). Organized information relating to the orientation of the earth in still older times does not as yet warrant confidence in any solution. Certainly no paleobiogeographic evidence known to me requires drift of either poles or crust. In the event of stepwise polar shifts, moreover, one might expect to be able to identify structurally the concurrently shifting path of the equatorial bulge, which should have been a site of stress, and evidence indicating drastically variant magnetic polar positions in post-Paleozoic times requires either very abrupt displacement and return of the earth's rotational axis or theoretical innovations that will permit the real or apparent magnetic poles to wander independently of the rotational axis.

The satellite program will be a geologic success if it provides data for a new theory of rock magnetization. The best hope for a clear solution to the ultimate problem of crustal drift, however, lies in more and better paleobiogeography, especially for the Paleozoic sediments and in the ocean basins.

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Biogeographical Boundaries: The Shapes of Distributions

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MANY of you will be familiar with pictures showing distributions of animals and plants which appear to be related sensibly to the distribution of other organisms or of some measured feature of the environment or of some geological character. Such pictures are mostly taken from studies of terrestrial ecology, occasionally from fresh or brackish water or from work at the edges of the sea, from the intertidal zones. But all of us who have worked on marine problems know that there are boundaries in the middle of the ocean which are sometimes as sharply defined as the boundaries between sea and shore or between wood and meadow. The need for charts of distribution in the open ocean was recognized by the American National Academy of Sciences whose Committee on Oceanography has produced a most enlightened and ambitious series of documents under the general title *Oceanography, 1960 to 1970*. In Chapter 3, on "Ocean Resources" the committee reports that:

> There is a great need for continual, systematic mapping of the oceans. This should show quantitatively, by seasons, the geography of the various elements composing marine environments . . . . Its practical application would be to predict the location of promising fishing areas and the probable abundance of fishery resources therein.

The Committee referred to "continual biological surveys to measure the ever-changing abundance of exploited fish stocks . . . and map shifts in patterns of distribution."

Much of the present knowledge of marine biogeography was acquired in the course of the classical oceanographic expeditions such, for example, as the *Challenger* voyage in 1873–1876, or the *Meteor* expedition of 1925–1927. Further knowledge has been added from the normal working cruises of many laboratories. Special programs have sometimes been organized such as the cooperation between European laboratories from 1902 to 1908 which led to the important charts and notes on the distribution of plankton published by the International Council for the Exploration of the Sea.

All these surveys, however, were of limited duration, mostly lasting from one to three years, or were dependent on sampling at irregular intervals of time and space from ships using a variety of collecting gear. The distributions which are charted from such sources are static; that is, there is little or no information about gradients of abundance, or of seasonal and annual changes in the location of the center or range of distribution of an animal. Or as Hedgpeth (1957a) has said, "much of the current literature of biogeography is . . . systematic and historical rather than ecological in its approach." On the other hand, Darlington (1957) criticized the tendencies to make zoogeography a subdivision of ecology and to glorify historical zoogeography at the expense of the study of present "static" distributions.

The attempt to draw fine distinctions between the two subjects seems to me to be as unprofitable as discussing whether biochemistry is biology or chemistry. Ecology and biogeography are no more than convenient words for overlapping and ill-defined disciplines, each of which contributes toward knowledge about biological processes; they provide tools which can be distorted or molded into new shapes for each new problem. Many problems in ecology can be answered only from a knowledge of the dynamics of distributions.

The difficulty of sampling pelagic organisms has led to a special weakness in the present static distributions, which usually show, by dots on a chart, all the positions in which an organism has been captured. Frequently the location of these dots appears to reflect the activities of the great expeditions or the proximity of a laboratory rather than any biological character. Those of you who feel this is an exaggeration should compare Walford's (1958) picture of the world distribution of marine laboratories with Steuers' (1933) picture of the distribution of the copepod *Anomalocera patersoni*. The two charts are almost indistinguishable.

The dispersal of communities on the land, in lakes, at the edge of the sea, and on the sea floor is often limited by physical barriers. Because of this, terrestrial or benthic animals and plants may usually be assigned, with some precision, to a particular type of fauna or flora. Frequently, terms may be chosen which describe the factors limiting distribution; for example, brackish, littoral intertidal, or desert.

Because there are so few barriers to their dispersal, pelagic communities are not so easily classified and it is difficult, if not impossible, to use the word "community" with any precise meaning. I shall use it rather loosely and not necessarily with the implication of interdependence of the animals and plants described in this way.

Throughout this paper, the word "distribution" has been used to refer to the geographic location of gradients of abundance. Many biogeographers would use distribution to describe the geographic range or limits within which a species is normally found. In ecology, however, distribution and abundance cannot be separated; as Andrewartha and Birch (1954) have said "they are but the obverse and reverse aspects of the same problem."

These problems of classification and nomenclature are intensified by one of the most interesting characteristics of pelagic organisms. To quote Ekman (1953), "At the boundary between two faunal regions the conditions of flow may on certain occasions bring about a change in the composition of the plankton and certain plankton species are thus indicators for various types of water."

With these difficulties in mind, it is highly desirable that dynamic biogeographical studies shall be based on standardized methods of sampling applied over long periods of time. Such consistency is useful in defining the limits of distribution of species and communities, but its greatest value lies in the quantitative expression of migrations and other fluctuations in abundance and distribution, and the study of their possible causes and effects.

The systematic collection of physical and chemical data is becoming routine and, recently, there has been an improvement in the recording of commercial fishery statistics. The techniques of fisheries biology were discussed at a symposium of the member countries of the International Commission for the Northwest Atlantic Fisheries at Biarritz in 1956. Reporting on this meeting, Lucas (1958) wrote, "Attention was drawn to our relatively scanty knowledge of the ecology of the plankton and particularly of the distribution of the eggs and larvae of commercial fish . . ." .

I shall concentrate on the plankton, therefore, although similar remarks could be made about all forms of marine life. Most of my material is taken from the Continuous Plankton Recorder Survey. I have done this partly because the survey is carried out from my own laboratory in Edinburgh and partly because it provides an example of a standardized method of sampling used over a long period of years.

Some Examples of Shapes of Distribution

Nearly all the illustrations which follow are taken from the work of Mr. J. M. Colebrook and Mr. G. A. Robinson who are making a special study of the dynamics of the distribution of plankton based on the Recorder Survey. I am indebted to these two colleagues and also to Dr. M. H. Williamson for many suggestions and discussions.

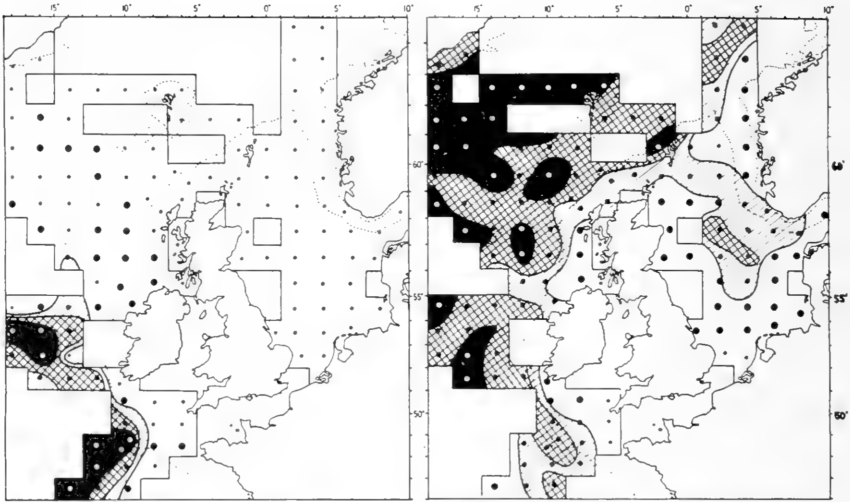
The Continuous Plankton Recorder was designed for use from commercial freighters on their normal sailing schedules (Hardy, 1939). It is towed at a depth of 10 m, sampling the plankton continuously on a moving band of bolting silk. From 1932 to 1939 it was used mostly in the North Sea, but after World War II, the sampling was gradually extended to include a comprehensive cover of the northeastern Atlantic. This was made possible by the introduction of the Ocean Weather Ships which began to tow Recorders in 1948.

The Recorder Survey has provided an opportunity to study many aspects of the plankton over a very wide area. In 1957, we decided that the accumulation of material taken during the nine years 1948 to 1956 was sufficient to provide an estimate of the "average" distribution of plankton—an atlas which we could use as the biogeographical background for further studies of annual and seasonal fluctuations in the abundance and distribution of individual species and of groups, or communities, of organisms. The "average" distribution is the resultant of seasonal and annual fluctuations of many diverse factors. Our objective was to discover the faunal and floral patterns or shapes of distribution. Similar objectives have been pursued by, for example, Bieri (1959) working on the chaetognaths, Brinton (1959) on the euphausiids, Rass (1959) on the commercial fisheries, and by Bogorov (1958), and many other Russian workers on a variety of organisms, mostly in the Pacific.

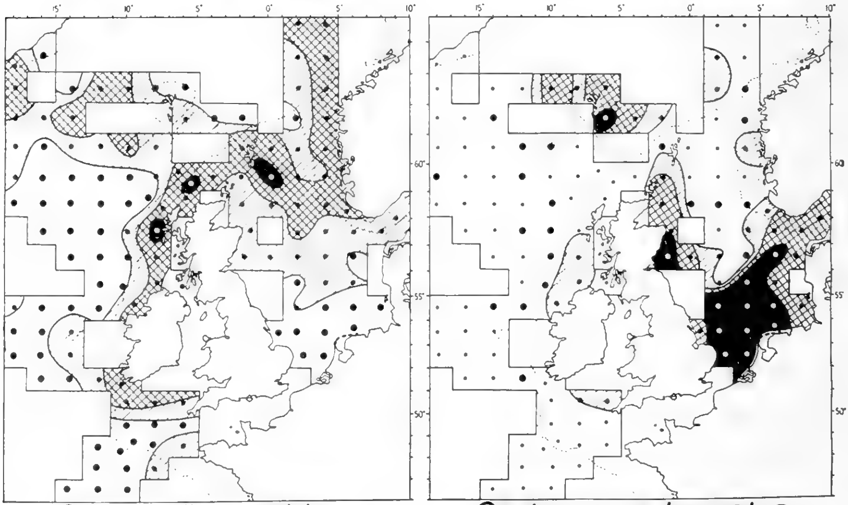
As far as possible, every Recorder route was sampled once a month; for examples, see John and Brown (1958). The records were divided into sections, each representing ten miles of towing and bearing the plankton from about 3 m^3 of water. Each of these 10-mile samples was assigned to a geographic square, and contours of equal abundance were interpolated between the centers of the squares, based on the nine-year average number per sample of each organism. The distributions of more than sixty species of diatoms, dinoflagellates, copepods, gastropods, tunicates, and young fish were prepared in this way to form a contribution toward an atlas of the plankton of the northeastern Atlantic and the North Sea (Colebrook *et al.*, 1961).

Figure 1, which is taken from this atlas, shows the distribution of four species, ranging from those found only in the oceanic parts of the survey to those restricted to the coastal regions and the North Sea.

A striking feature of the distribution of many species was the close correspondence between the contours of abundance and the position of the continental slope as defined by the 100-fathom depth contour. Some organisms were abundant over deep water but scarce or absent over the continental shelf (e.g., *Calanus minor*



Calanus minor *Thalassiothrix longissima*



Calanus finmarchicus *Centropages hamatus*

Fig. 1. The average distribution and abundance of four species taken in the Continuous Plankton Recorder Survey. The contours are based on the average number per sample during the nine years, 1948–1956; they are drawn at abundance intervals of ×3. Small dots indicate the centers of sampled squares in which the organism was absent; larger dots show that the species was recorded in small numbers (Colebrook *et al.*, 1961).

or *Thalassiothrix longissima*). Others were abundant over the shelf but showed a sudden decline in numbers at the position of the 100-fathom contour; for example, *Calanus finmarchicus* which followed the line of the continental slope around the British Isles but also reflected the position of the relatively shallow waters of the Wyville-Thompson Ridge between Scotland and Faroe and northwestward across to the Icelandic shelf. The change in the abundance and species composition of the plankton in the region of the 100-fathom contour is so marked that it is frequently possible to detect the position of the contour by a visual inspection of the Recorder silks.

As was to be expected, the distribution of a number of organisms appeared to reflect the inflow of oceanic and coastal water from the Atlantic into the northern North Sea. For example, *Thalassiothrix longissima*; this, and similar species, were found in the Atlantic and, extending by a tongue, into the North Sea. Other species, with their main centers of distribution in the southern North Sea, appeared to retreat from this tongue of Atlantic influence (see *Centropages hamatus*, Fig. 1).

No attempt has been made, in this atlas, to describe the distributions in the conventional terms of biogeography. The different organisms may be fitted more easily into a continuous series than into separate types of distribution. In Fig. 2 (from Colebrook *et al.*) the plankton has been listed in such a series, the position of each organism being dependent on the location and extent of its abundance and distribution in the Recorder Survey. Each species was distributed in a similar way to its immediate neighbors in the list.

Although the series is continuous, it is possible to divide it into a number of loosely defined parts. A large group of organisms tended toward an *oceanic* distribution; a smaller group was largely, but not exclusively, *neritic*; and a third group, showing distributions between and overlapping these extremes, can be described for convenience as *intermediate*. Moving along the series one moves progressively toward or away from *oceanic* through *intermediate* to *neritic* distributions. All these terms are relevant only to the Recorder Survey; they were selected as being useful and descrip-

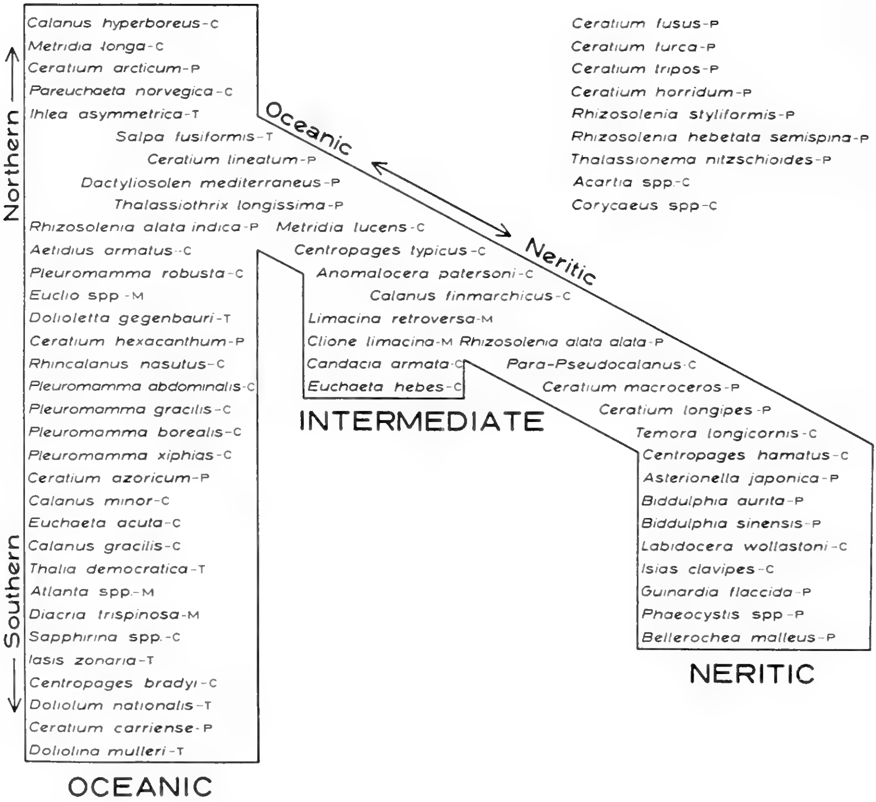


Fig. 2. A biogeographic series for the northeastern Atlantic and the North Sea, derived from the Continuous Plankton Recorder Survey. The organisms are arranged so that the distribution of each species is similar to that of its neighbors in the series. P, phytoplankton; C, copepods; M, molluscs; T, tunicates (Colebrook *et al.*, 1961).

tive without any implication of the mechanisms which may determine or limit distribution.

A small fourth group does not fall easily into the series and is unclassified; it contained four species of dinoflagellates, two diatoms and two copepods. All of them were widely distributed and they showed many of the expected features, such as the gradients of abundance parallel with the continental shelf. It is possible that they were ubiquitous within the area of the survey, but preliminary investigations suggest that it is more likely that they were species with a number of geographically separate populations.

Darlington (1957) pointed out that "wherever regional faunas meet or are separated by partial barriers, there is transition, overlapping of faunal elements, with progressive subtractions in both directions." He classified organisms as *exclusive* (belonging to one fauna), *transitional* (belonging mostly to one but extending into the neighboring fauna), and *shared* (belonging to both faunas). The terms used in this list, *oceanic*, *neritic*, *intermediate*, and *unclassified*, can be related approximately, to fauna A, fauna B, transitional, and shared in Darlington's Fig. 53. It is extremely difficult, however, to define separate faunal or floral groups in the plankton; transition occurs in all directions within and between the *oceanic*, *neritic*, and *intermediate* groups of organisms. The boundary between *oceanic* and *neritic* is usually read as the position of the 100-fathom depth contour. This criterion has been relaxed somewhat, in preparing this list, in order to preserve a distinction between those organisms found only over the North Sea plateau and those found mainly over the Atlantic shelf to the west of the British Isles. Some of the distributions described as *intermediate* would probably be classified as *neritic* by other workers. Braarud *et al.* (1953) and Smayda (1958), in their biogeographical studies of marine phytoplankton, also found neritic and oceanic to be unsatisfactory terms. Smayda came to the conclusion that they should be discarded as being ill-defined and unrelated to the factors controlling the distribution or the life cycle of the phytoplankton species. He proposed, instead, a binary classification based on the life cycle (*meroplanktonic* or *holoplanktonic*) and on the distribution. He classified distributions as *anoictic* (Greek, in the open sea), *paractic* (Greek, of the coast) and *adiaphoric* (Greek, indifferent). The operation of this scheme is dependent on the recognition of those waters "modified by coastal influence" or "free from coastal influence." It is doubtful whether the present state of knowledge is sufficient to render this distinction less ambiguous than the previous division between *oceanic* and *neritic*. The three divisions used in the present series, however, are probably fairly close to Smayda's classification. But, with the exception of a few organisms with very restricted distributions, none of these terms can be applied too rigidly to the plankton. It is for reasons such as these that Fig. 2 has been prepared as a continuous series with the addition of the noncommittal terms *oceanic*, *neritic*, and *intermediate*.

Hitherto, planktonic indications of water movement have usually been sought from the evidence about a few relatively rare organisms. But there is an appreciable hazard in the deduction of water movements or other environmental changes, from observations of a single species. The distribution and abundance of an organism reflect many factors of mortality and survival, or aggregation and dispersal, of which water movement is only one. It seems likely that some of these difficulties would be reduced by studying the total species composition, and it should be possible to make use of information about the common species which make up the bulk of the plankton and which are, perhaps, most important in studies of fluctuations in the commercial fisheries. Abramova (1956) studied the abundance and species composition of the plankton as part of an ecological study of the herrings of the North Atlantic. She described cold and warm water forms in the plankton and was able to demonstrate the value of a wide variety of species in providing biological indications of water movement.

Indications of environmental change or water movement in different parts of the Recorder Survey would be provided by groups of organisms selected from different parts of the series. For example, in studying conditions in the northern North Sea, groups of organisms at the *oceanic* end of the *intermediate* series would be compared with species from the upper end of the *neritic* series. In Glover (1957), I attempted to use the species balance of the plankton in this way. Figure 3 shows my earlier results brought up to date.

During the past ten years samples were collected, with the Hardy Plankton Indicator, by fishermen taking part in the summer herring fishery in the northwestern part of the North Sea, a fishery which lies in the path of the inflow of water from the Atlantic. From

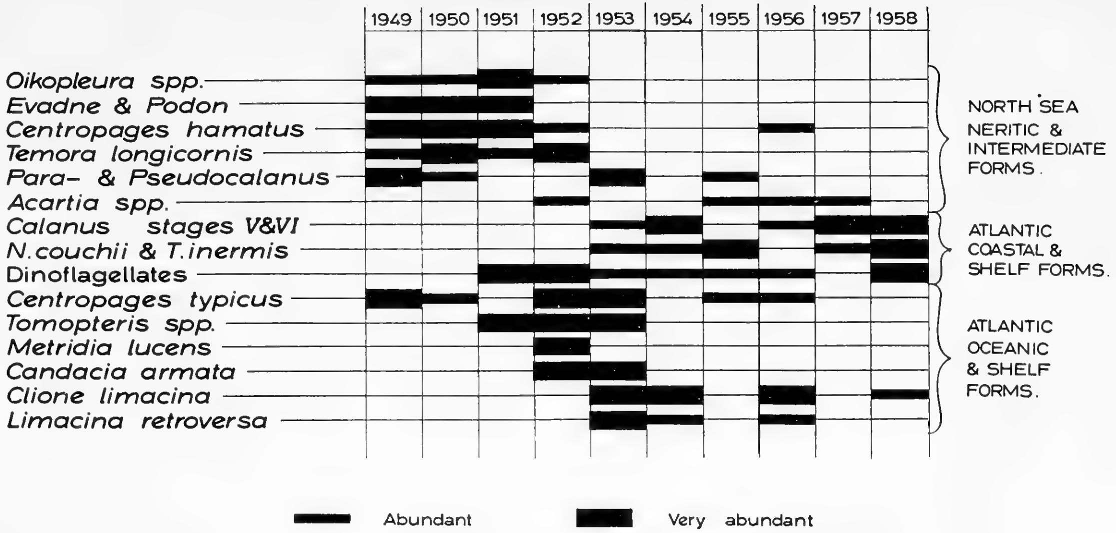


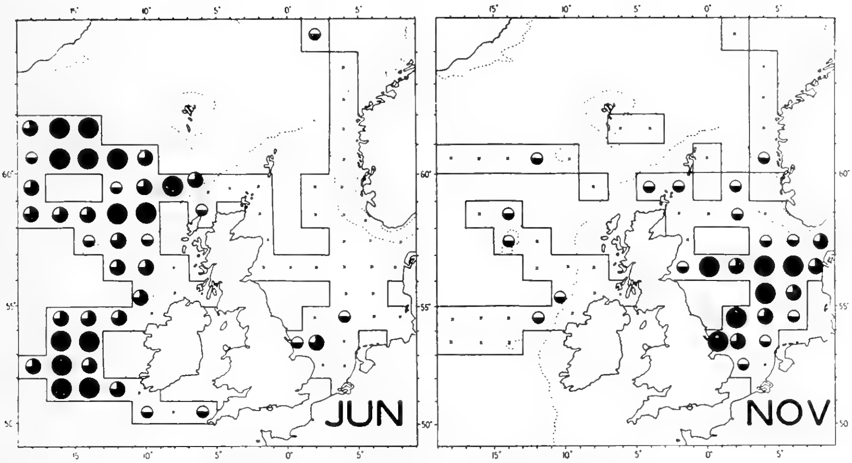
Fig. 3. The relative seasonal abundance of the plankton of the northern North Sea herring fishing grounds, from material collected by fishermen using the Plankton Indicator. Organisms were classed as abundant when their numbers exceeded the 10-year average for at least a third of the season; when they exceeded twice the 10-year mean for a third of the season, they were classed as very abundant (Glover, 1957, brought up to date).

this material a biogeographical series was compiled, rather like the one shown (Fig. 2) for the Recorder Survey but much smaller. It begins at the top with ubiquitous and typical North Sea neritic species, passing through organisms characteristic of mixed North Sea and Atlantic shelf conditions to species (at the bottom) from the mixture of oceanic and shelf water.

It is immediately apparent that there were three major periods in the plankton. From 1949 to 1951, the North Sea neritic forms were abundant but they then declined and the more oceanic organisms increased in numbers during the years 1952–1954 and 1956. In the two years 1957 and 1958, there was a decrease in this plankton and an increase of the species whose "average" distribution pattern was intermediate between the North Sea types and the oceanic shelf mixture.

It would be outside the scope of this paper to describe the fishery in detail, but I should mention that the importance of these phases in the plankton is that they were contemporary with three phases in the fortunes of the herring fishery. From this I formed the hypothesis that the success or failure of the Scottish summer herring fishery is partly dependent on the inflow of mixed Atlantic oceanic and shelf water into the North Sea (Glover, 1957).

To return to the shapes of distribution: In order to expand the static background provided by the Recorder plankton atlas, Colebrook and Robinson have charted the average monthly distributions during the same period of nine years; that is, all samples taken during the nine Januaries or the nine Februaries were combined to provide one picture for each month. Many organisms showed remarkably static distributions throughout the year; others showed a progressive advance and retreat of their distribution patterns as the seasons passed. But some showed marked seasonal trends and changes which were repeated in each year. Figure 4 provides an example compiled from the nine-year average distributions; it shows the two extremes of the seasonal distribution of *Rhizosolenia styliformis*. As I suggested above, the most likely explanation of patterns of this kind is that they result from the existence of two biologically separate populations, or stocks, or races of a species.



Rhizosolenia styliformis

Fig. 4. The average distribution and abundance of the diatom *Rhizosolenia styliformis* in June and November. The charts are based on the combinations of these months during the nine years 1948–1956, in the Continuous Plankton Recorder Survey. Crosses indicate the centers of sampled squares in which *Rhizosolenia* was absent or scarce. The three sizes of circles are drawn at abundance intervals of approximately ×3 (G. A. Robinson, unpublished).

Although most organisms were distributed in a similar way in each successive year, there were differences between years, some of them abrupt and some showing trends of changing distribution. One example is provided by the mollusc *Clione limacina* which, between 1948 and 1952, was found over the deep waters of the Atlantic. Thereafter, in each successive year, its distribution became progressively restricted toward the continental shelf until in 1956 it was almost entirely confined to the shallow waters around the British Isles. Figure 5 shows the two extremes of this trend and, like Fig. 4, offers a convincing argument for the repetition of routine sampling over long periods of time. A striking instance of changing distribution on the seashore is provided by the barnacle *Elminius modestus* in European waters (Crisp, 1958).

Another aspect of the shape of distributions concerns the seasonal timing of the biological cycle of each species. Many organisms showed a consistent history with the same *season* of abundance in each year and about the same *level* of abundance in each season. But some species underwent emphatic changes such as those il-

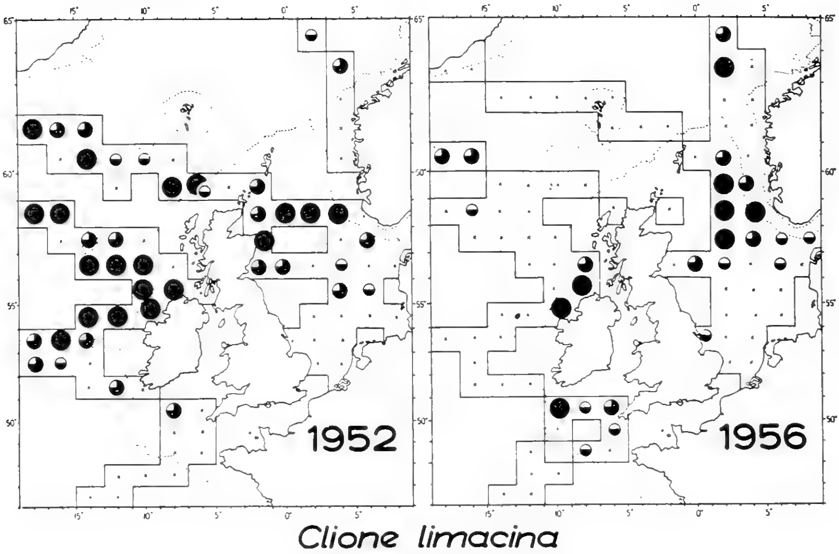


Fig. 5. The average distribution and abundance of *Clione limacina* in 1952 and 1956, based on the Continuous Plankton Recorder Survey. Crosses indicate the centers of sampled squares in which *Clione* was absent. The three sizes of circles are drawn at abundance intervals of ×3 (F. R. Vane, unpublished).

lustrated in Fig. 6, which shows the seasonal timing and abundance of a diatom (*Thalassiothrix longissima*) and a copepod (*Corycaeus anglicus*) in the North Sea during the last ten years. *Thalassiothrix* was relatively rare until 1952 but subsequently it became a common and most consistent part of the plankton in the winter and spring. *Corycaeus* showed the reverse trend; appearing regularly during the late autumn between 1949 and 1953, it was almost absent from Recorder collections during the last four years.

These two pictures help to emphasize one of the limitations of plots of static distribution ranges which I mentioned above. Both species were found in the same area, in this example, the North Sea. But, because of their different biological seasons and because of different between-year trends they would hardly ever meet each other in the sea.

Inspection of the temporal shapes of distribution such as those in Fig. 6 showed that there was one kind of seasonal cycle in the

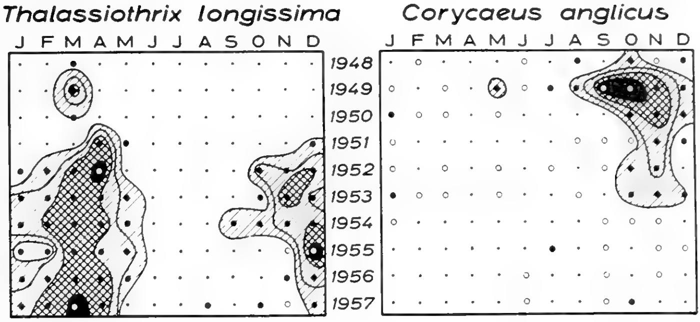


Fig. 6. The seasonal abundance of a diatom (*left*) and a copepod (*right*) in the North Sea, based on the Continuous Plankton Recorder Survey. The contours are based on the average number per sample in each month. Small dots indicate that the species was absent; open circles, large dots, and the contours are drawn at abundance intervals of ×2 (G. A. Robinson and J. M. Colebrook, unpublished).

plankton over the deep Atlantic part of the Recorder Survey and a different cycle in the shallow waters of the North Sea.

Figure 7 summarizes this difference for the most common species of phytoplankton and copepods. It is based on the period of nine years, 1948 to 1956; that is, the nine Januaries, etc. It is not a community succession diagram in the usual sense as it does not show dominance in the plankton but only the successive seasons of each species. In the southern North Sea there was a marked sequence of peaks of abundance of both phytoplankton and copepods; the total effect is one of biological activity throughout most of the year. In the Atlantic, on the other hand, the sequence was less marked; nearly all species showed the same period of abundance and the general impression is of a biological season shorter, by two or more months, than that of the North Sea. Other methods confirm this result and suggest that the difference is largely explained by the earlier spring outburst of diatoms in the North Sea and by the relatively small autumnal phytoplankton crop in the Atlantic. The seasonal cycles in both parts of the survey were much more protracted than those found by Kielhorn (1952) and Fish (1954) at the ocean weather station in the Labrador Sea, at about the same latitude as the Recorder Survey.

Figure 8 illustrates another aspect of long-term fluctuations in

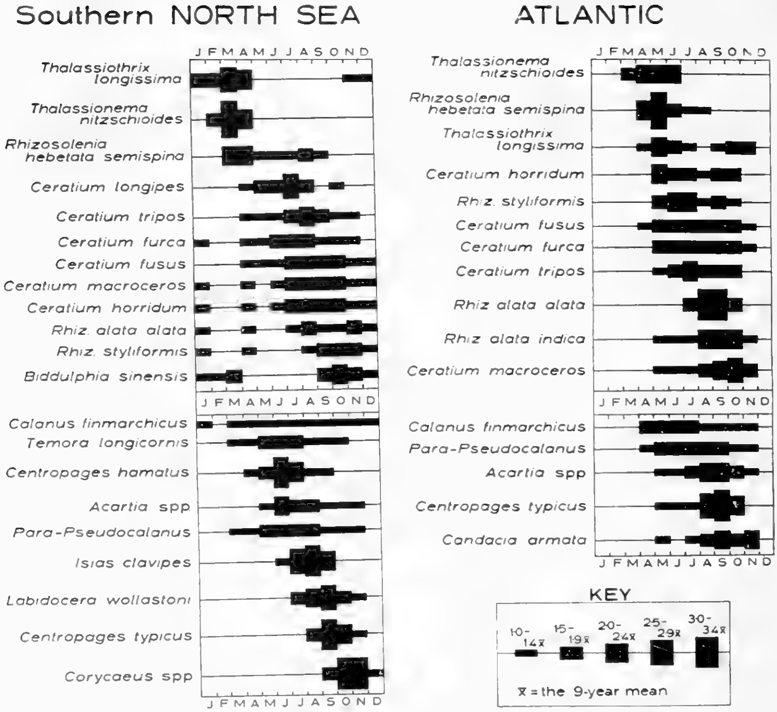


Fig. 7. The average abundance of the common species of phytoplankton (above) and copepods (below) in the southern North Sea and over the deep Atlantic part of the Continuous Plankton Recorder Survey. The histograms are based on the combination of like months during the nine years 1948–1956. The height of each monthly histogram indicates the abundance of each species related to the average number per sample (of that species)for the whole period of 9 years (G. A. Robinson and J. M. Colebrook, unpublished).

abundance which I mentioned above. It shows the mean number per sample, year by year, of *Calanus finmarchicus* and two species of *Ceratium* in the southern North Sea. It is at once clear that the *Ceratium* species fluctuated in a closely similar manner, and that the numbers of *Calanus* varied in a different way which was to some extent the inverse of the pattern shown by the *Ceratium* species.

By calculating correlation coefficients between all possible pairs of species, Colebrook and Robinson have found that there was a

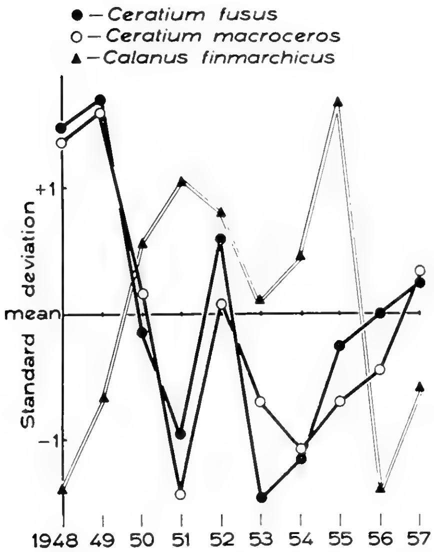


Fig. 8. Annual fluctuations in abundance of two dinoflagellates and a copepod in the southern North Sea, taken with the Continuous Plankton Recorder. The average numbers per sample are expressed on a common measure scale about the mean number for the whole period of 10 years (G. A. Robinson and J. M. Colebrook, unpublished).

relatively small number of patterns of abundance fluctuations of this kind. From an analysis of a matrix of correlation coefficients it should be possible to establish which groups of organisms fluctuated in similar or in opposed ways. This is an extension of the technique of determining associations between species from a matrix of coincidence of pairs of species in a group of samples.

Figure 9 shows another application of the study of these annual fluctuations in abundance. I should explain that one of the most interesting events in the herring populations of the southern North Sea was the increase in length which occurred in 1950. Cushing and Burd (1957) showed that this was contemporary with an increase in the abundance of *Calanus finmarchicus*, an important food of the herring. The lengths of the fish remained high, and the *Calanus* continued to be abundant until 1956 when a drop in the length of the herrings was coincident with a fall in the numbers of *Calanus*. This is illustrated here, by using the mean length of three-year

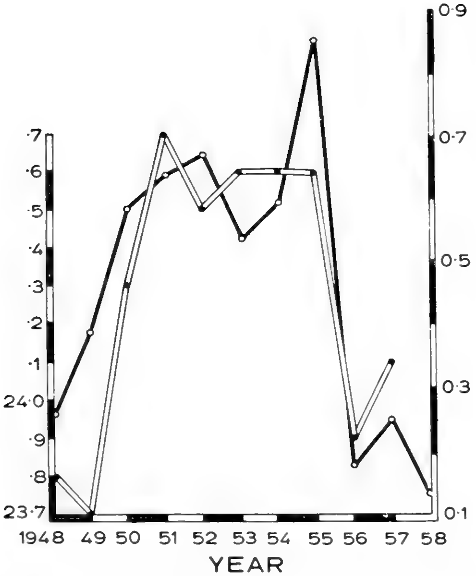


Fig. 9. Herring and plankton in the southern North Sea. The open line (scale at left) shows the mean length of 3-year-old herrings in the East Anglian fishery (data provided by A. C. Burd of the Fishery Laboratory, Lowestoft). The solid line (scale at right) shows the logarithmic mean per sample of *Calanus finmarchicus*, stages V and VI, in the Continuous Plankton Recorder collections in the southern North Sea during the months February to July of each year (J. M. Colebrook, unpublished).

old herrings and the numbers of *Calanus* in the Plankton Recorder collections in the southern North Sea in those months when the herrings were feeding. It suggests that the supply of food during their first three years of life influences the length of the herrings. This kind of result is a most rewarding proof of the value of long-term sampling.

All the shapes of distribution and abundance which I have shown so far have been based on a geographic scale or on a time scale, but, in ecological studies, the position of a species may be fixed by factors, other than geographic ones, which may influence distribution and abundance. Dr. B. M. Bary, when he was in New Zealand, plotted the occurrence of planktonic species on to a temperature salinity diagram. He was able to determine which species would be likely to act as indicators of different water masses and, from the distribution of these species, he estimated the origins of the different components of mixed water (Bary, 1959a).

He has continued this technique in Edinburgh and Fig. 10 shows the application of the method to the Continuous Plankton Recorder material. The results for the months of August and September, 1957, have been combined. A large number of temperature and salinity observations were available from routine sampling aboard commercial freighters, ocean weather ships and research vessels. From these a *T/S* diagram was prepared for the Atlantic part of the survey, the central North Sea, and the shelf waters, including the western entrance to the English Channel. The boundaries of the water masses were drawn in the usual way. Many of the ships taking these salinity and temperature observa-

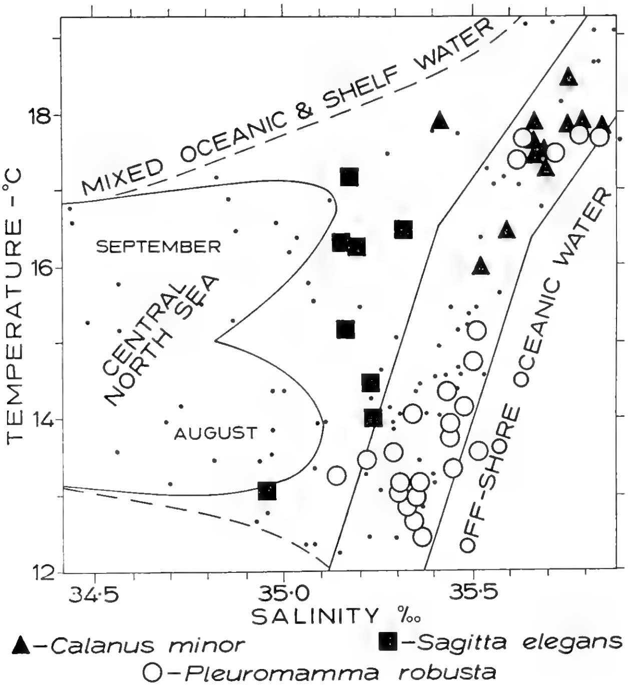


Fig. 10. Temperature-salinity-plankton diagram for the northeastern Atlantic and the central North Sea during August and September 1957 (modified from Bary, 1959a).

tions were also towing Plankton Recorders. Each dot or symbol indicates the position of a Recorder sample. The presence of three species is shown. It is clear that the separate distributions could be explained in terms of the tolerance of these species to environmental conditions or of their recruitment from different water masses. The boundaries between the water masses corresponded to the boundaries between the distributions of the plankton. Two of the species were confined to the off-shore oceanic water. One of them (*Calanus minor*) was restricted to the warmer part and the other (*Pleuromamma*) was found mostly in the colder end of the oceanic water but with some overlap into the warm water. The third species, *Sagitta elegans*, occurred over a wide temperature range but only in the mixed shelf water; it is, of course one of the best-known indicators of the presence of Atlantic coastal water in the North Sea. None of these three species was found in the central North Sea during these two months. This is a very simple example, taken from Bary (1959b) and is chosen to illustrate the potentialities of this method of expressing the shape of distribution.

Concluding Remarks

It would be tempting at this stage to consider other techniques by which distributions could be related to various characters of the environment. It is impossible to generalize, however. A great variety of valuable work is already being carried out, and different techniques meet the needs of different situations. A few examples will suffice. Brandhorst (1958) has shown an inverse relationship between the depth of the thermocline and the size of the standing crop of plankton in the eastern tropical Pacific. A little further west, in the central Pacific, King (1954) has shown that upwelling (resulting from the equatorial divergence) provides nutrients for the phytoplankton and, through the zooplankton, for the tuna which is so plentiful in this region. In the benthos, Vinogradova (1959) has related zoogeographical regions to physical features such as underwater ridges. Taylor *et al.* (1957) have shown the long-term relationship between climatic trends and the distribution of pelagic fish and lobsters in New England. Crisp (1958) has shown that the spread of the European distribution of the barnacle *Elminius modestus* may be partly explained by transport on the hulls of ships; and that *Balanus amphitrite* has become established near the warm effluents of electricity power stations in Britain (Crisp and Southward, 1959).

I have, therefore, done no more than provide examples of different aspects of the shape of distribution and abundance in time and in space without any reference to environmental factors which may be related to these distributions. The point I want to make is this: that the ecologist who wishes to extend his work beyond the limits of local exploration and who aspires to study fundamental principles of general importance will need quantitative estimates of abundance, distribution, and species composition of the kind which I have shown. The fact that my examples were taken from the plankton of a limited area is irrelevant. The same requirements will apply in studies of the seashore or the bottom of the ocean.

We are all aware of the limitations of isolated cruises but most marine biogeography is based on the findings of surveys or expeditions which were isolated in time, space, and technique. At the symposium on "Perspectives in Marine Biology" held at Scripps in 1956, there was an impressive number of pleas for repetition of sampling of coral reefs, on the shore and in the open sea.

I suggested earlier that repeated surveys using standardized techniques are necessary. I mean "standardized" within one program and throughout its duration. I would not advocate universal standardization of sampling methods, although this may be possible in some fields, and it has already been achieved in the physical and chemical recording of such factors as salinity, temperature, and oxygen.

Sampling methods will obviously depend on the nature, size, and abundance of the organisms that are to be captured. Most studies of the dynamics of distribution will be served better by many, frequent, small samples than by a smaller number of large ones. Some research will be needed in each project to discover the size of the smallest sample which will yield useful information.

Gulland (1955) has made the case for small samples in the study of commercial fish populations.

Hedgpeth (1957b) wrote that "the most significant aspect of the intertidal populations of sandy beaches, at least in temperate latitudes, is its fluctuation." I would have thought that this was true of all marine life and that all the major problems facing ecologists are concerned with the mechanisms of stability and change in the sea, problems which can be solved only by a study of fluctuations whether they be short-term, long-term, seasonal, annual, spatial, or temporal.

It is obvious that results must be expressed in quantitative terms so that changes in abundance and distribution can be measured and compared. This usually means making a count of some kind. "Quantitative," however, is not a synonym for "accurate" in the sense of "precise." Whatever the temporal or spatial frequency of sampling, the interpretation of the results will involve processes of interpolation and extrapolation which may sometimes be closer to acts of faith than to scientific methods. The largest samplers take extremely small subsamples of most marine populations and, from what we already know of variation in the sea, the estimation of population parameters from even the most unbiased of samples is a hazardous business.

With these points in mind careful thought should be given to the desired accuracy of the techniques. It is necessary to ensure that the time-consuming practice of accurate counting does not add useless refinement at the expense of frequency of sampling. In the Plankton Recorder Survey we have compromised between counting and estimating the abundance of organisms; for instance, the number of a species in a subsample is expressed as lying between 5 and 11, or 26 and 50, or 251 and 500. Such categories for estimates of abundance must be chosen with care so that they do not inhibit the subsequent mathematical treatment of the results.

A further problem in the design of surveys of distribution and abundance is concerned with the techniques of identification of organisms. Many useful contributions have been made from a knowledge of the total weight or volume of organic matter, or from the total standing crop of animals or the total green pigment. Some of the most interesting results in the Recorder Survey have been obtained from a visual inspection of the green color of the silks, using this to provide a crude estimate of the distribution of phytoplankton. Another useful technique for gross estimations is provided by the C^{14} method. On the other hand, it may sometimes be necessary to discover the specific identity of each organism. Obviously the choice of detail in this matter lies with the objective of each investigator. But knowledge of the generic and specific name of an organism may sometimes give a false sense of precision in ecological work. This arises from the dependence of studies of population dynamics on the recognition of "unit stocks" within the species population. Mr. B. B. Parrish of Aberdeen has studied this aspect of fisheries biology and (in a private communication) he defines a unit stock as a subgroup of a species which is self-contained biologically, with its own population parameters of reproduction, growth, and mortality, and which can be treated dynamically as independent of other subgroups of the species.

It is often necessary, therefore, to break a species down into separate homogeneous population units, and it may be significant that the greatest complexity of subdivision of this kind has arisen in those organisms which have received most attention from biologists; for example, the herring *Clupea harengus* and the copepod *Calanus finmarchicus*. The recognition of separate population types is often dependent on a statistical examination of a large number of individuals in a sample; see, for example, Hill (1959) on American shad. It is possible in some areas to assign an individual herring to one or another type by the recognition of differences in the otoliths (see Parrish and Sharman, 1958). Cushing (1955) followed the changing distribution of separate populations of *Calanus finmarchicus* by detecting differences in size frequency diagrams. But as Parrish has said, the concept of unit stock does not imply any particular taxonomic status.

Nevertheless, ecologists and morphologists could profitably work together to maintain the utility of nomenclature and to prevent an unwise multiplication of new species and genera. There is an excellent opportunity for such collaboration in the study of the world populations of *Calanus* and related genera about which a lot of new information has emerged in recent years.

In the examples I have chosen, and indeed throughout ecology, there is an implied emphasis on the study of what Hedgpeth called "ecological units or communities." As I have suggested, it is extremely difficult to define and classify communities of pelagic organisms. Indeed, Allee *et al.* (1949) did not confine this difficulty to the pelagic zone; they argued that all the components of marine life are interdependent and they treated the whole of marine ecological associations as a single major community. On the other hand, some workers have used "community" to describe any assemblage of species found in the same place, without any implication of ecological relationships.

Distribution, abundance, and species composition are to some extent parts of a continuously variable system, but we all know that certain combinations of species occur more frequently than other combinations and that the organisms in such groups are a fairly constant part of each other's biological environment. It is impossible to complete the study of the ecological relationships of a species without reference to the other organisms with which it lives.

The approach to the study of associations between species owes much to the techniques of the psychologists who have faced the problem of grouping various measures of human performance. The statistical techniques known as *cluster analysis* or *factor analysis* have been used. Many of the tests depend on the calculation of *correlation coefficients* of various kinds which are then assembled into a matrix from which similar and dissimilar groups can be selected, preferably by some objective test. Kontkanen (1957) has described some of these techniques. The terrestrial botanists have been concerned with the same problem of continuity or discontinuity of vegetation; for example Poore (1956) and Goodall (1953, 1954). Fager (1957) devised an *index of affinity* between species and showed how *ranking methods* and *concordance analysis* could be applied to the study of various interspecific relationships. Margaleff (1958) discussed the problems of temporal succession and spatial homogeneity in the phytoplankton. He referred to the so-called *diversity indices* dependent, in various degrees of complexity, on the ratio between the number of species and the number of individuals, in a sample or an area. From such an index he was able to provide geographical plots of heterogeneity of communities of phytoplankton.

The application of these techniques to ecology is only just beginning, and many difficulties remain to be solved. Most tests of affinity or association between organisms have been dependent on the presence or absence of species in a sample or a quadrat. There are weaknesses in this approach which is unduly sensitive to sampling errors and to variations in sample or quadrat size. The groups of concurrent species determined from small samples will frequently be different from those found in large samples.

But there is no reason why these methods should be applied only to the presence or absence of species. We have already started to use them in Edinburgh in the analysis of similarity or dissimilarity of patterns of long-term fluctuations in abundance, and they could be used also in the grouping or separation of genetic or morphological features.

Biologists of all kinds are attempting to carry their work from the study of individual organisms into the study of natural populations and communities. In making this step, mathematical techniques of the kind I have mentioned will be most useful. But success will be limited unless the results can be based on repeated sampling. More careful attention must be paid, in the future, to two technical problems; the design of field equipment and the design of field surveys.

Biologists have sometimes been accused of collecting too much material. It may be that, for oceanic biology at least, they have not collected enough.

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Evolution in the Deep Seas

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MY object in this paper is to compare the conditions of evolution in terrestrial and deep-sea environments and to discuss how far the peculiar characters of the deep-sea fauna can be ascribed to the conditions of their environment. I shall restrict myself to the general features of deep-sea evolution and not discuss the special adaptations of members of the fauna. Before making the comparison I must first summarize the views of evolution, and especially microevolution, to which recent work leads. This I shall do, and then pass on to discussion of evolution in the deep seas.

One of the most striking features of almost all land and fresh-water environments is the extremely local distribution of the conditions that determine where a species is to be found. The presence or absence of a species at any point is often determined by such local features as the presence of a plant, the shade of a tree, or a log at some special stage of decay. Even when an environment is homogeneous in its general features—a pinewood, a heather moor, or a desert—most species are not found everywhere in the environment. Only the species associated with the dominant plants are generally distributed; others are found in small areas within the environment where the conditions are particularly favorable to them. It is not only on this small scale that the distribution of animals in terrestrial environments is discontinuous. On a larger scale such an environment as a grassland or a wood is usually separated from other environments of the same kind by regions where the conditions of life are different and therefore unsuitable for the fauna of the grassland or wood. On a still larger scale an island or the upper parts of a mountain may be completely isolated from other similar environments.

Freshwater environments are even more generally discontinuous than land environments. Whether a piece of freshwater is large or small—a lake, a pond, or a pool of water in a gutter—it is always separated from similar environments by land or by dissimilar aquatic environments such as a stream or river with conditions to which the fauna of the lake or pool will not be adapted. The result is that by far the greater number of terrestrial and freshwater species are distributed in local populations isolated more or less completely from other populations of the species. Both the size of the local populations and the degree of their isolation are greatly variable, but it is only some of the most highly locomotory species, some birds, some insects, and the larger and especially the carnivorous mammals, that may not be distributed in these local populations. In these species the population may be reduced to single breeding pairs or families. These local and more or less isolated populations have been called "demes."

There must undoubtedly be in general some migration, active or passive, between the demes; otherwise new habitats suitable for the species would never be colonized. But recent work has shown that the distances over which animals wander are less than might at first sight be thought. Small mammals such as field mice or lemmings do not wander more than 50–100 yards from their homes, and among the less active invertebrates snails have been found to move not more than 5–10 yards in a year. The isolation of the demes is therefore real, though it is not often complete.

From the point of view of the study of evolution, the interest of these facts lies in the realization that it is in the demes that differentiation is initiated. Provided the isolation is sufficient, two demes will evolve independently so long as they remain isolated from each other. For estimates of the sufficient grade of isolation we have the work of Sewell Wright (1943), who shows that a mutational difference of selective advantage $1/n$* will evolve independently in two populations if the migration between them is not more than $1/n$ per generation. Complete isolation is not

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* An advantage of $1/n$ means that $n + 1$ individuals bearing the mutation survive to the next generation for every n individuals without it.

essential, and migration may be more frequent the greater the selective advantage of the mutation. Also, fixation of neutral characters in the populations of the demes may occur if the demes are small. The estimate usually given for the maximum population in which this can occur is 1000 individuals. Fixation of neutral characters may be important in giving an explanation of the occurrence of the large numbers of apparently neutral, and usually trivial, characters in natural species. It is unlikely that the more important characters on which the progress of evolution mainly depends can ever be neutral.

These local demes will hardly ever be sufficiently permanent to allow new species, or even recognizable new forms, to be evolved in them while they remain isolated. Almost always, as the result of change in the environment, they will come into contact with other demes before differentiation has gone far enough for the populations to be described as new species or subspecies. But when two demes fuse owing to breakdown of the isolation between them, any mutational differences between them will be preserved in the fused deme if they are advantageous, and neutral characters may persist if the size of the fused deme is not too large. In repeated fusions over the range of the species, characters will spread through the range, and the genotype of the species will gradually evolve.

Where some part of a species is *permanently* isolated from the rest, it will continue to differentiate until it forms a new subspecies or even species. We then get a *divergent* type of evolution distinct from the *successional* type in species with undivided range. In a large undivided range slowness of diffusion may result in the characters of the species differing in parts of the range, or the environmental conditions may so differ over the range that adaptational differences occur in the different regions. In both these cases we get a *cline*, a gradual change of the specific characters over the range. All these types of evolution should be distinguished.

This is the general theory of microevolution in terrestrial environments to which recent work on the ecology of animals has led. It refers only to bisexual animals. If the reproduction is nonsexual, the process of evolution will be very different; lineages each descended from a single ancestor will compete with each other and the most efficient will survive. There will be no opportunity for the spread of mutations from one lineage to another. Such species must depend entirely for their evolution on the occurrence of mutation in the separate lineages. The scheme I have outlined, besides according with the known ecology of animals, has the advantage of accounting for both divergent and successional evolution. It also allows us to understand how the many apparently nonadaptive characters that are found in natural species, and often distinguish one species from another, can be evolved in the presence of selection.

There is another character of many terrestrial environments that seems important for a comparison of the process of evolution in them and in the deep sea. We are living in an exceptional period of the world's history. It is only 12,000–20,000 years since the retreat of the ice at the end of the last glacial period, and on both the geological and evolutionary time scales that is a very short period. Whether the Ice Age is wholly over, or the present is an interglacial period after which the ice will again advance, is for our present discussion unimportant. In either case it is clear that climatic changes have been great and rapid in the last 20,000 years, much more so than in the longer, more stable parts of the world's history. In temperate regions the most important climatic changes have been in temperature; in the tropics temperature has probably not varied greatly either during the Ice Age or after it, but there have been large variations in rainfall. The amount of rain is in the tropics the most important condition controlling the distribution of animals, and its variations must have had almost as marked effects on evolution as those in temperature in the cooler regions.

Animal evolution has undoubtedly been largely affected by this unusual instability of climate. The most obvious effect has been to increase the rate of evolution. Change of the conditions to which an animal is exposed will always lead to rapid change in its adaptations, provided that it is able to survive the change, for the direction of selection will be altered and the animal's characters will alter in response to the new selection. In fact, stability or instability of the environmental conditions is the most important factor in control of the rate of evolution.

The instability of the postglacial climate will have affected the evolution of animals in other ways. Environmental changes alter the distribution of species, and their frequency will determine how often local populations lose their isolation by coming into contact with other populations of the species. Instability of the climate will therefore make the spread of variations through a species more rapid and increase the rate of its evolution for this reason also. It seems, then, that the recent history of land and freshwater faunas should have been one of rapid evolution. This is borne out by observation. To take a single example, there is the case of the char (*Salvelinus*) in the lakes of northern Europe. These fish have differentiated into numerous forms of at least subspecific grade, each in a different lake, and this differentiation must have taken place since the lakes were uncovered by the retreat of the ice. In more stable periods similar differentiation has been found to take hundreds of thousands of years (Zeuner, 1946).

In any comparison of marine with terrestrial environments the first thing to be said is that the marine environments are of almost as many different kinds as the terrestrial. In the littoral regions the environments may be as locally variable as those on land. So far as the distribution of species is concerned, evolution of much the same kind as in terrestrial environments is to be expected and, I think, occurs. I shall not discuss the littoral region. Then, again, it must be remembered that the sea is three-dimensional, whereas terrestrial environments are for most animals two-dimensional. The conditions of planktonic, pelagic, and benthic life differ in the deep sea as much as in shallower waters. I shall, however, not try to distinguish the conditions in these modes of life but to consider whether any general conclusions can be drawn about evolution in the deeper waters of the sea.

Several features of the environment of the deep sea seem unlikely to modify fundamentally the evolution of the fauna. The low temperature will slow the whole tempo of life and therefore, presumably, its evolution, but there is no reason to think it will alter the type of the evolution. The external and restricted supply of food will control the density of the fauna but should not modify the type of evolution except by encouraging the development of food-gathering adaptations. The high hydrostatic pressure should have still less effect. The absence of light reduces the food supply by exclusion of plants and will lead to adaptations for life in a dark environment, with emphasis on olfaction and bioluminescence, but, again, it will not modify the evolution of the fauna in any fundamental way.

A factor which has probably had a much more general effect on evolution in the deep sea is the greater homogeneity of the environment over wide areas than in terrestrial or littoral environments. Recent work may have shown that the abyssal floor is not so generally composed of featureless plains as we formerly thought, but it is surely true that local differentiation of conditions is much less on the abyssal floor than in environments where plants are plentiful. In the benthic fauna there will be less general separation within species of local and isolated demes, and the presence of currents in the water above the bottom will lead to the same result by increasing the distribution of the fauna. In fact it is difficult to see how any of the causes of isolation effective on land will be operative on the sea floor except distance isolation. For pelagic animals local differentiation of conditions will be still less.

We should therefore expect that the recent evolution in the deep sea should be less rapid than on land, and perhaps that the number of species formed should be fewer. This is what we find. Ekman (1953), for instance, emphasizes the wide distribution of abyssal species and the absence of local forms. On land, distance isolation often results in formation of clines and they might be expected to occur also in the deep seas. But clines will not always be formed in widely distributed species. Even though the isolation is mainly by distance, it need not be wholly so, and specific differences may be evolved in isolated parts of the species range. Owing to further environmental change species so formed may later come into contact as sympatric sibling species. In fact such closely related sympatric species do occur in the deep seas (e.g., species of *Stomias*, cf. Marshall, 1954, p. 343), though they seem to be less frequent than on land, perhaps not surprisingly. Finally, since the interbreeding populations will be wider, and probably contain more individuals, there would seem to be less possibility of neutral characters being evolved. I do not think our knowledge of the deep-sea fauna is detailed enough to allow us to say whether this is so or not. Even in terrestrial faunas it is always difficult to say whether a character is really neutral or has some value in the biology of the animal.

Deep-sea environments differ from the terrestrial in another respect: the recent Ice Age will have had much less effect upon them. Extension of the polar ice cap must have caused some latitudinal change in the distribution or temperature and perhaps of currents, but it can hardly have altered conditions greatly in other ways. It would seem that the deep-sea fauna cannot have been subjected to the large environmental changes and consequent rapid evolution to which the terrestrial fauna has been subjected in its recent history. In the deep seas there must have been long periods of more stable conditions, stretching back at least into the Tertiary, in which the fauna evolved to its present condition. In this period most of the specific characters of the fauna will have been evolved. This conclusion is not negatived by the fact (Menzies and Imbrie, 1958) that archaic forms are not numerous in the deep seas. That they are not more numerous is perhaps surprising for one might have expected many such forms to find there refuges in which they could survive. The hope that this might be so was one of the reasons why the original *Challenger* expedition was organized. But the reason must lie in the earlier history of the oceans, a subject I cannot discuss.

The recent stability of the deep-sea environment may explain another striking feature of the fauna. In some groups of which many of the fishes are the most obvious example, but some of the cephalopods and holothurians should also be included, we find fantastic modifications of the form of the body and great differences between closely related species. The great development of the mouth and stomach in some of the gulper eels (*Saccopharynx*, etc.) and the forms of the body in some ceratioid angler fishes are well-known examples, but some of the forms of the holothurian group of the Elasipoda might equally be quoted. All these are greatly developed examples of adaptive radiation, for there can be no doubt that they are adaptations to the special needs of the animal's life, in the fishes chiefly to the need of gathering food. Equally fantastic adaptational modifications are found in some land animals; the peacock's tail and the feathers of the bird of paradise are examples, and there are many among the insects. These also are clearly adaptive to the animals' biology, but their use is more often in sexual display. In land animals they are occasional and do not occur in considerable proportions of whole groups as they do in the deep-sea fauna.

The land animals which show these astonishing forms are closely adapted to restricted modes of life. They are, in fact, highly specialized animals, their specializations serving particular aspects of their biology. In most environments specialization is dangerous. If an animal is adapted only to life in a narrow niche, it is exposed to the danger that the niche may cease to be available as the result of environmental change. If it has very specialized habits, the adaptations needed for these may make it inefficient in other ways. If either of these happens, the animal will perish unless it is able to readapt rapidly. Specialization, therefore, will always be checked by selective forces when it becomes too extreme, but up to this point there will be active selection toward greater elaboration of the specialized adaptations since this will lead to greater efficiency for their uses in the biology of the animal.

The stability of the deep-sea environments and the fact that variation in the environmental conditions is less local than on land will have reduced the dangers of specialization and allowed it to be carried farther. Also, the long and relatively unchanging history of the environment will have given plenty of time for the elaboration of the specializations, even though evolution may have been slower than it would have been in a more variable environment. It is to be noted that on land most of the animals with fantastically developed specializations occur in the tropical forests, probably the most stable and one of the oldest of terrestrial environments.

The changes in animal biology that constitute evolution depend on reaction between the animal and its environment. It is therefore to be expected that the process of evolution will differ in its details, if not in its more fundamental characters, when unlike environments are compared. There is always a tendency in discussion of a broad subject such as evolution to lay the emphasis on the more accessible parts of the subject and to disregard other parts which cannot be investigated so easily. This is certainly true of the study of evolution, for by far the greater part of the modern theories of evolution has been founded on observation and experiment in terrestrial environments. It therefore seemed worth while to point out that the modern scheme need not necessarily apply in its details to all environments. The deep sea and the land, being environments as different as any to be found in the world today, seemed well adapted to establish these points by a comparison of the process of evolution in them.

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The Role of Ethology in Oceanography

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SOME hold that biology has no place in the science of oceanography; and it may be recalled that in the early stages of the negotiations leading to the formation of the British National Institute of Oceanography the first draft list of its personnel included, among *many* oceanographers, only *one* biologist. He was to act as liaison officer and was to be given a comparatively junior standing.

Once biology is admitted into oceanography the whole range of organismic activity has to be let in for consideration. The situation is like that of a large, ungainly, infant cuckoo in the nest of another and smaller kind of bird with differing and more tidy habits. Yet, although biology is likely to make great demands on oceanography, it has also big things to offier as is quite clear from the nature of the seminars and of other biological lectures at this Congress. Among these offerings are ethological findings.

The term "ethology" in the title of this lecture was not chosen lightly. There must surely be something a little odd about a subject upon which the leading encyclopaedias (even in their latest editions) are silent; about which the principal dictionaries are ill-informed; which, as a subject, does not appear in *Biological Abstracts*, *Psychological Abstracts*, the *International Abstracts of Biological Sciences*, or the *Catalogue of the International Library of Medicine*. Yet the subject is hotly debated, arouses strong enthusiasms in its followers and neglect and contumely from others, and has an international journal of comparative ethology called *Behaviour*. This unsatisfactory situation arises partly from etymological confusion with *ecology* and partly through the misguided labeling of one particular school of the study of animal behavior as ethology.

The etymological confusion may be illustrated and perhaps clarified by a brief account of a controversy which took place in 1902. Prof. F. W. Very (1902, p. 473) asserted, "Scientific descriptions remain unintelligible to the lazy man who hates to use the dictionary; they are free property to all who are willing to take this trouble."

A correspondent, Horace White (1902), then Editor of the New York *Evening Post*, wrote in the next number of *Science* that he had decided to vindicate himself against this charge of laziness, and so had looked up two words which had appeared in the same number as that in which this statement was made. The words he selected were "ecology" and "ecological." He found, in fact, that, so spelt, both were absent from the dictionaries he consulted, naming Webster's, Murray's, and others. The Editor of *Science* confirmed (1902, p. 511) that these words could not be found in these foremost authorities and asked for help. There were replies from prominent dictionary editors and a long correspondence followed in which Bather and other leading zoologists took part, ending in an essay by Wheeler (1902).

Several points emerged from all this:

1. The two words *were* in the dictionaries quoted but under the letter O, and were shown as beginning with the dipthong œ; the noun *œkologie* having been first used by Haeckel (1866) in his *Generelle Morphologie.*
2. Although The Madison Botanical Congress, 1893 (23 and 24 August) had recommended that the anglicized spelling *ecology* should be adopted and had given its definition as "broadly the study of all forms of adaptations of organisms to their environment," this anglicized spelling had not found its way into the dictionaries.
3. There was confusion among some French and German writers about the meaning of *œkologie, biologie,* and *ethologie,* and a tendency to equate them.

Pearse (1939) rightly wrote that "at the beginning of the twentieth century ecology was a young, but an established, science, and such eminent ecologists as Wasmann (1901), Dahl (1901), and Wheeler (1902) were discussing whether Saint-Hilaire's *ethology* or Haeckel's *ecology* should be used to designate the science of relations of organisms to environment." Allee *et al.* (1949, p. 42) also quote this and regard it (as indeed it is) as a correct summing up of the position in 1900. They point out that Saint-Hilaire conceived of ethology "as including 'the study of the relations of organisms within the family and society in the aggregate and in the community' " and go on to say "it has been argued that since the character of an organism is revealed only through its reaction to its environment, there is no essential difference between human and other aspects of 'ethology,' " thus linking its etymology to its earlier English usage, revived by John Stuart Mill (1843), as "the science of human character."

It may surprise those who speak of "ethology as a new branch of biology" to hear it suggested that ethology as an English word with a zoological connotation first appeared in the original edition of Parker and Haswell's well-known textbook of zoology (1898). There they wrote: "The whole question of the relation of the organism to its environment gives us a final and most important branch of Natural History which has been called Ethology or Bionomics" (Vol. I, p. 9). This sentence remained unaltered up to the fifth edition (1930) and is quoted as illustrative material in the Supplement to the *Oxford English Dictionary* (1933, p. 343) but both the word "ethology" and the sentence disappeared from Parker and Haswell in 1940 when Lowenstein carried out a revision of the text of Volume I for the sixth edition. "Bionomics" they owed to Ray Lankester (1889) and "ethology" (in this context) to Saint-Hilaire (1859).

Wheeler (1902) rounded off the discussions by an essay in which he discussed the three words—biology, ethology, and ecology—at some length and concluded that "the only term hitherto suggested which will adequately express the study of animals, with a view to elucidating their true character as expressed in their physical and psychical behaviour towards their living and inorganic environment is *ethology*." He wrote (Wheeler, 1902, p. 975):

> The word "ethology" is singularly happy in its derivation from ἦθος, which embraces in the wealth of its connotations, all the aspects of the zoological discipline for which a concise and appropriate name is so

> much needed. The origin of the word ἦθος from ἔθος custom, usage, is clearly given in Aristotle (*Ethica Magna*, II 6.2; Ethica *Endemia* II, 2.1, Ed. Bekker). The general Greek usage of ἦθος, especially in the plural ἤθη, as the accustomed seat, haunt, habitat, or dwelling of men or animals, admirably expresses the chorological aspect of "ethology"; its usage in the sense of habit, manners, etc. (lat. consuetudo, mores) expresses what we mean by animal behaviour, while the signification of ἦθος as character, disposition, nature, etc. (Lat. *indoles*, *ingenium*, *affectus*) is well suited to express the psychological aspects of "ethology." Certainly no term could be more applicable to a study which must deal very largely with instincts, and intelligence as well as with the habits and "habitus" of animals. It is apparent from a moment's reflection that the term may be readily made to include all and more than is meant by "Biologie" in the German sense, or "œcology" in the Haeckelian sense.

Although intended to clarify it seems likely that Wheeler's essay may be partly responsible for some of the loose speaking about ethology and the varying interpretations put upon the word itself.

J. Arthur Thomson introduced *ethology* into the *Zoological Record* for 1901 as a subsection of "I. General Subjects . . . 4. Physiological . . . d. Nervous and Sensory: Comparative Psychology . . . Ethological"; but in that for 1902 (following Wheeler's essay) David Sharp, who had taken over this section from Thomson put "Ethology" into the comprehensive section while still retaining "Comparative Psychology" in general zoology. This situation lasted until the *Zoological Record* for 1939 when it disappeared altogether as an index subject. No one who regarded some of the subjects included by Sharp in ethology would be surprised at the contents of Pelseneer's (1935) monograph *Essai d'ethologique d'après l'étude des Molluscs*, yet it contains hardly a phrase of ethological treatment as now defined or as generally understood.

The concept of *ecology* (from Gr. *oikos* = house, habitat environment), however, has now definitely crystallized out of this mix into the more quantitative or numerical aspects and physicochemical interrelationships of organisms with their environment and with each other. This leaves *ethology* completely free to be used for the study of the behavioral aspects of these relationships and such others as are generally comprehended in the terms comparative psychology and comparative behavior. It is important that it should become widely recognized that this discipline really means, as Thorpe (1958) also says, "*the scientific study of animal behaviour*," and not merely, as Eibl-Eibesfeldt and Kramer (1958) say, "an approach to the study of animal behaviour, derived from the study of *instinctive* movements." This restricted definition is the basis only of the so-called modern ethology associated particularly with the names of Lorenz, Tinbergen, and Baerends, but which is equally the basis of many other schools of comparative psychology or behavior.

At this point it had been the intention to give a general account of the development of modern ethology and its concepts, but at the Scripps Institution (1956) Symposium on *Perspectives in Marine Biology* Thorpe (1958) gave such an account and how he visualized its possible development in the field of marine biology. It is therefore neither necessary nor desirable that this ground should be gone over again.

Lehrman (1953) and Kortlandt (1955, 1959) especially have criticized the claims and concepts of the modern ethologists, and Schneirla (1952) and Aronson (1957) and others have cautioned against the uncritical acceptance of their causal explanations.

Nonetheless the Lorenz school of ethology has brought into sharp focus and tried to systematize many behavioral phenomena which do not fit readily into existing psychological or physiological explanations of organismic activity. It has also brought into prominence procedural techniques which ought perhaps to have been adopted long ago and for reasons quite different from, but complementary to, those given by themselves.

If one takes a small area of shore, plots its microclimates, as expressed in terms of temperature, lengths of exposure, type of rock surface, slope, currents, etc., then notes the numerical distribution of an animal or various animals occupying the different niches and so establishes a mathematical relationship, this is *ecological* work. But if, either in the field or in the laboratory, one tries to find out why an animal seeks these situations, or studies what it does in unusual circumstances designed to disclose the behavioral or, if you like and speak more loosely, psychological factors motivating its ability to, shall we say, rise above, or come to terms with its environment, then this is *ethological* work. Some ecologists, however, notably Elton, have recognized the limits set on ecological deductions by lack of behavioral data.

Both of these approaches, conjoined with neurophysiology and other biological disciplines are of course needed in the attempt to comprehend fully an animal's whole relation to its environment or neighbors; but they all demand very different techniques and need different degrees of emphasis according to the stage at which scientific knowledge finds itself, but especially they need different types of mind to study them.

Consider now the biological aspects of oceanography and, in particular, those with which the independent marine laboratories are concerned. These laboratories may be held to be responsible for seeking out the fundamental facts upon which rational exploitation of the sea for the greatest good of the community may be based, and for providing the operational research scientist in government departments with a sound basis upon which to build. This is the main justification of their support from public monies allocated mainly for the purposes of development. Let us take stock briefly.

It is a little over a century ago since scientific marine biology got underway. It rightly gave up much time in the early stages to collection, description, and systematization. In European waters at least we know the eggs and larvae of almost all the marine fishes and a good deal about the stages in the life histories of most things that live in the sea; we are in a few messes over nomenclature, but perhaps not bad ones; we have got together a vast amount of ecological and physiological—though almost no ethological—data; and we certainly know something about the harvest from the sea in terms of material returns from certain expenditures of effort and cunning. Of this catalogue of achievement the community as a whole is probably only much concerned with the last. This harvest, in so far as it consists of such things as fishes, whales, crustaceans, and molluscs, is dependent mostly on the congregation of these various animals in diverse ways at certain times and places where they may be caught, either there or in passage there.

We do not yet know why or how these congregations take place with any single marine animal, in the same sure kind of way that we have this knowledge of some land animals.

Now, a man can go from one end of a street to the other in many ways. He can be pushed or pulled, run, skip, leap, or dance down it; he can be blown down it by wind or blast or carried down by flood; his motives in going down it may be due to attraction, repulsion, or compulsion; if these motives are powerful enough, as in battle, he may exert sufficient effort in this act of passage to go to his death; and lastly, if he is a whole man the sensory factors guiding him down the street will be very different from those he would use if he were blind or deaf.

Out of this very small catalogue of causes, some are clearly beyond his control, others are partly within his control, and others are the result of his own choice, operated through a perceptual field. Normally, his journeys down the street will be the latter, and the others would have no real bearing, or if they had, could be analyzed and assessed.

There is no reason why it should not be the same with animals in the sea. At certain stages, or for some transient physical reason, animals whether adult or larval may be forced from place to place by forces beyond their control; but for the most part the movements of importance to them are directive (not necessarily "goal-seeking" as some ethologists would have it), the result of attraction, repulsion, or compulsion, occasioned and maintained by perceptual data. The study of these factors, whether instinctive or learned, is part of ethology.

It is wasteful at this stage of the development of the science of oceanography to continue to formulate hypotheses of an ecological nature without first establishing their ethological basis. Dr. Verwey (1959) gave close consideration to some of these factors and summarized present knowledge of both passive transportation and active displacement of marine animals, relating his observations to behavioral data, so far as they are available. He dealt with a wide range of organisms and with some of the hypotheses about those migrations which contribute toward the congregation of animals in certain places and in certain ways. But he did not deal with one of the most striking aspects of these and that is the characteristic of so many marine organisms and economically important fishes of living together in shoals or schools. Neither does this challenging subject receive treatment in Margaret Brown's (1957) *The Physiology of Fishes.* This is not a phenomenon of interest *only* to the biologist. No matter for what purposes echo-sounding or Asdic devices are used, the presence of this type of congregation can be either illuminating or complicating, or both. The ethological mechanisms by which the schools are brought together, held together, or dispersed, or by which they can be induced to be so held or dispersed, could have an immense significance both economically and militarily.

Now, Steven (1959) has shown experimentally, under laboratory conditions, that in two shallow water shoaling tropical western Atlantic fishes, *Hepsitia stipes* (Müller and Troschel) and *Bathystoma rimator*, shoals disperse when light intensity falls below about 0.1 ft-c, but that they also disperse with similar behavior patterns when stimulated olfactorily by weak solutions of various tissue extracts. He makes a number of interesting speculations such as that "it seems equally likely that the fish learn to associate the regular diurnal changes in light intensity with vertical movements of their food and, having become so conditioned, continue to respond to the light stimulus even when not feeding. Another possibility is that non-feeding as well as feeding fish may continue to follow the concentration gradient of substances liberated by plankton in their diurnal vertical migrations." These speculative conclusions from his paper are quoted here, not with acceptance or approval, but merely to show how packed with unanswered ethological questions these two inoffensive sentences really are. They are very typical of discussions on the ecology and behavior of marine organisms. Further examples can be found in many of the papers in several sections of this Congress. Zelikman (1959) drew attention to a well known phenomenon and that is their keeping together by groups which maintain their general identity under a number of disrupting circumstances, and she attempts an explanation in terms of "reflexes" and mechanical action of currents. Dr. Jenner (1959), on the other hand, discussed schooling behavior in the marine snail, *Nassarius obsoletus*, and dealt directly with the environmental factors responsible.

It is time now to ask: Can useful and valid inferences be drawn from ethological observations on oceanic animals made under restricted aquarium conditions?

As the outcome of suggestions made at a meeting of the International Council for the Exploration of the Sea at Amsterdam in 1951 (Bull, 1952) a research assistant, Miss V. M. Brawn, joined me at Cullercoats to make a study of the behavior of *Gadus callarias*, the most important commercial fish of European waters. What follows is the result of a joint endeavor but is mainly her work. It is put forward here to illustrate the kind of ethological approach which can be profitably used in the study of economically important marine animals. We have already reported briefly upon it (Bull and Brawn, 1959) and further papers will shortly be published by her.

Patient observation over two years of large numbers of healthy specimens (ranging in size from 7 cm to 70 cm), many of which lived throughout the period of observations and were known as individuals with their own code letter, enabled Miss Brawn (1957) to establish a number of ethological facts which have relevance to this discussion. There is time to summarize only a few of these. Cod develop a social hierarchy and an order of dominance through aggressive behavior which has not been previously described. This occupies a large part of their daily life. It includes a number of subsidiary actions, a fast approach, and a full threat display, and variations in their intensity; per contra there are the intimidating effects produced, such as flight and fear postures of the socially inferior individuals. Loud grunts of a frequency of less than 50 cps either singly or in 2, 3, or 4 often accompany aggression and flight; these again have not been described before but they are a significant feature of the cod's daily and seasonal activity.

Aggression is at its peak in late summer and autumn, and there is another outbreak during February and March at actual spawning time. At the times when there is no aggression, from after spawning to the beginning of July and again from December to the end of January mature fish swim freely in all parts of the aquarium without exciting aggression. During aggressive periods fish which are being continually put to flight by other more aggressive ones come to show fear of these in other situations. A dominated fish swims out of the way of an aggressive fish even when it is not displaying or threatening. They learn each other's status so that a fish can threaten those lower in the hierarchy without being threatened in turn. An order of supersedence or precedence thus develops, and this is related to the order of dominance.

The order within the community was consistent and suggested to Miss Brawn that the fish knew each other individually and were aware of their status in relation to others. The average distance at which one fish of a pair erected its dorsal fins (a sign of fear) and moved out of the path of slowly approaching but nonthreatening "superior" fish was 36 cm, the maximum 122 cm.

Some changes took place with time, and the relative status of the more dominant was occasionally reversed, but by and large the aggressive nature of individual fish and the order of dominance retained the same characteristics from one year to the next, in spite of a long summer period when aggression and differences of "social level" were absent.

Both sexes are aggressive during the peak period of aggression in the autumn and indiscriminately against each other; but in the immediately prespawning time aggression is shown only by the males and against other males and unripe females.

A number of large fish were closely studied during the 1957 spawning, from 4–15 March. Three weeks before this period the dominant male fishes set up territories, which they defended against all intruders. Differential responses were given to fish entering the territory and so far as could be seen these were based solely on the behavior of the intruding fish. If a female ready to spawn or approaching spawning condition entered the territory she did so relaxed, swimming slowly, and showing no fear. Males did so quickly, reacting quickly to threat display by returning it, by flight, or other fear responses.

Once the sex of the intruder is recognized as female the male "flaunts" or "displays" at a distance of about a foot, and if the female is ripe and ready to spawn the sequence is "flaunting" followed by curious movements accompanied by prodding and grunting for some 10–15 minutes, actions all directed toward driving the female *upward.* They culminate in a pseudocoitus or ventral mount during which eggs are discharged and sperm shed. Actual spawning behavior was seen to occur only when the light was so dim as to make observations difficult, and it should also be added that territories were not apparently defended or maintained during darkness.

Now it is of the essence of the ethological program that observations made upon animals in captivity are vital adjuncts to those made in the field. There is good reason to assume that the primary behavior patterns of such animals as the fish we have just described are not different under healthy conditions in a well-run aquarium from what they are in nature. What then can be said of the cod in nature from what we have seen by close observation in the aquarium?

Dominant males exclude other males and immature and spent females, but *not* females on the point of spawning, from a territory they have established. Prespawning aggression, leading to territory formation, starts 3 to 4 weeks before females are ripe for spawning. This would give time in nature for weaker males to be sorted out. The territorial preserve around every dominant male would permit the behavioral sequence leading to spawning to take place without interruption and so help to ensure maximal fertilization.

Spawning occurs between February and May. The spawning shoals are said to lie at between 40 and 100 m. In captivity the courting behavior of the male drives the ripe female *upward,* while aggressive behavior drives unripe females and other less vigorous males downward and away from a defended territory. It is possible then to think of cod gathering in the spawning areas at the bottom in water of, say, 150 to 200 m. The aggressive and courting behavior patterns would lead to horizontal layering of shoals or groups of fish, with ripe females at some comfortable "ceiling" (the surface of the water was of course the "ceiling" in the aquarium), the dominant males slightly below or with them, and unripe and other males in the lowest layers. During all this, much display and grunting would be going on. After spawning is over, aggression, including grunting as part of the display, ceases and they pass each other quietly.

The other and main period of intense aggression which comes in late summer and early autumn, and which gives rise to dominance and dispersal of either sex by both sexes would lead to the dispersal of individuals at small distances from each other thus ensuring for each fish a better chance to get food.

Of importance to all these ideas is the finding that grunting (whether in courting or aggressive display) only affects fish which are not more than 2 ft away from each other, and no evidence was found that it triggers off mass stimulation; and secondly, that the "flaunting" display, an essential component of natural courtship in the cod, seems to be a visual releasing mechanism, although it takes place only in crepuscular light. There can be no doubt that at these times of great aggression (September to November) and again at prespawning aggression as well as during actual spawning the ocean where the cod shoals are congregated must be full of the sound of cod grunts.

This suggests that the use of hydrophones to find cod would be of value, but only seasonally. But it also emphasizes that the accurate recording, identifying, and classifying of underwater noises of all kinds is an important section of the contributions which behavior study has to make to oceanographical problems.

Within the whole field of behavior research possibly no general class of experiments is so well known as those into the ability of animals to show insight into configurational problems, of which Koehler's investigation of the detour performances of chimpanzees is a classical example. Thorpe (1958) reviewed some of this work briefly so far as it relates to fishes. What it is desired to stress here is that this kind of study has relevance to the design of traps of all kinds used in the capture of fishes, crustaceans, etc., and that it could well lead to substantial modifications in design in traditional trapping techniques. Arising out of a general proposition to study configurational learning in the cod, Miss Brawn was led on to a general study of the ability of cod to learn detours. She has discussed and illustrated this additional avenue of exploration (1959).

The late Sir John Graham-Kerr, one-time Chairman of the Fisheries' Advisory Committee of H.M. Development Commission, repeatedly expressed doubts as to whether a decline in the catches of certain trawl fishes was indeed caused by overfishing, to which it was (and is) generally ascribed, or to some behavioral factor. It was at least a possibility, he thought, that a fish which had been a "near miss" in the net when it was small would learn from this experience and make an effort to avoid a repetition of the likelihood of capture. There was the further possibility that the then recently introduced widespread use of echo-sounders in trawlers was a contributing factor—again by the process of association—but in this instance of the regular onset of the sound with the arrival of the trawl. Against this was to be set the fact that there was no recorded example of any fish being able to detect sounds of these high frequencies.

Conditioning experiments of the kind described in the chapter on "Conditioned Responses" in Brown's *Physiology of Fishes* (Bull, 1957) therefore were carried out at Cullercoats into the ability of a number of fishes to perceive the sounds from two commercial echo-sounding transmitters, the Kelvin & Hughes MS 24 and MS 22, the first transmitting at a frequency of 14.25 kc/sec, the second at 30 kc/sec, the pulses in both going out at 66.7/minute. Neither of these transmitters submerged in the aquarium tanks and set transmitting at high intensity evoked any reaction or alarm or interest in any of the many kinds of fish then living in the aquarium, including a very high proportion of our common British food fishes.

These experiments showed that the fishes studied, *Blennius pholis* L., *Pleuronectes platessa* L., *Gobius minutus* Pallas, *Gadus virens* L., and *Gadus callarias* L., readily formed conditioned responses to 14.25 kc/sec and some of them also to 30 kc/sec. They therefore not only perceive these sounds but are able to use them in forming associations with other vital actions. This means that the suggestion that commercial trawl fishes might, by conditioning, become more wary of capture and, hence, lead to reduce catches cannot wholly be ruled out of consideration.

When one passes from the study of the behavior of adult animals relatively easy to keep and maintain to that of their larvae, ethology reaches its most vigorous challenge. First class work of this kind has already been done, though perhaps not consciously from this angle, e.g., Wilson's study of the factors affecting the settlement and metamorphosis of polychaete larvae (various papers, see Wilson, 1958). In all these problems of larval settlement, and some (e.g., fouling) are of great economic importance, there is the continual question: Do they settle in a certain spot because they choose to do so or because purely fortuitous circumstances compel them? How far can a fish larva come to terms with its environment as was asked earlier, by taking advantage of this eddy or that turbulence and with what success? The dispersal of fish larvae by wind-induced and other currents has been the subject of many papers, in which it has been generally assumed that the larvae are transported passively by and helplessly with the current. Bishai (1960), also working at Cullercoats, has established that even newly hatched herring (*Clupea harengus* L.) larvae orientate themselves into and are able to maintain themselves against current velocities of between 0.6 cm and 1.0 cm/sec and that against higher velocities they still orientate head into the current and drift less than the current velocity. There is clearly need for much more precise observation here and it might well be that the fine structure of the current systems of the seas are more important in larval distribution, through the stimulation of local effort, than gross pattern.

Only a few of the possibilities open to ethology of throwing light on biological oceanography have been indicated here. The modern ethologist, however, regards the exploration of innate behavior as the spearhead of his approach. In practical research terms this means first the drawing up of ethograms, systematic descriptions of instinctive movements (for example, Baerends and Baerends-van Roon 1950; Morris, 1958). This is an occupation which is not to everyone's taste, and for it to be successful there must be the enthusiasm and the patience to watch animals closely for long periods often under great discomfort. Moreover, if he is to occupy himself with marine animals, he will want more facilities for quiet observation than are at present generally available to him at the marine laboratories.

The need for this kind of work is becoming increasingly apparent and I would plead that at the major marine biological laboratories there should be added to the chemists, physicists, physiologists, algologists, zoologists, oceanographers, and hydrographers, etc., one of this new breed—an ethologist. He should, however, be encouraged to direct his research interests toward the behavior of animals of major economic importance and not be allowed to divert effort to smaller and perhaps more easily kept and studied species.

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Physiological Significance of Light in Marine Ecosystems

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GENERALLY speaking physiological research has two different aims: (1) it recognizes fundamental life processes within cells and protoplasm and (2) it assists in understanding the functional relations of organisms as a whole to their environment. In other words, the first objective of research is the individual organism itself, whereas the second is its relationship to environment. Naturally these are closely related and there is considerable overlapping between the two. However, different methods are necessary, and a clear distinction between them is possible. The title of this paper indicates that I shall deal only with the second aspect of the research, which may be called ecological physiology.

There are two methods used in ecological-physiological research. It is possible to find correlations between the appearance, distribution, abundance, and behavior of organisms and the distribution of environmental factors and their fluctuations. The parallel variations both of the organisms and of factors in their environment suggest conclusions that a given reaction depends on a certain factor. Vertical migrations of zooplankton, which parallel fluctuations in light intensity, provide a classic example for reasoning based on this sort of evidence.

Naturally there are many disadvantages in making such statistical comparisons. Only the more obvious interdependencies are detected, and exact information of physiological conditions within the organisms is lacking. Also, the method fails almost completely when reactions of the organisms are determined by several environmental factors. To some extent, these disadvantages can be overcome by laboratory experiment. In tests it is possible to vary one or more factors in the environment while keeping others constant either under optimal conditions or under any other controlled situation. Nevertheless, in determining ecological behavior, the value of the results obtained in this manner is limited for the following reasons: (1) biological factors, especially those due to the presence of other members in a biocenosis are lacking in an artificial environment; (2) it is impossible to reproduce the physical and chemical environments completely; (3) in nature, environmental factors represent an indivisible system. Alteration of any one factor, whether of biological origin or not, modifies all other factors.

Despite these reservations concerning this method, I believe that a combination of statistical comparisons and experiment will yield good results toward understanding biological correlations in the sea (Kinne, 1956).

Experimental physiological methods have been used for only a short time in marine biology. Recently, several problems have been solved experimentally. I shall give only a few examples: the work of Hardy and Bainbridge (1951), Moore (1950–1959), and Lewis (1959) on the vertical migrations of zooplankton; of Hauenschild (1955, 1956) on lunar periodicity of the polychaete *Platynereis dumerilii;* of Abbott and Ballantine (1957); and of Ray and Wilson (1957) on the poisonous effect of *Gymnodinium* in causing mass mortality of fishes; of Kinne (1959) on *Gammarus duebeni;* of Schlieper (1956; Remane and Schlieper, 1958) on osmoregulation in brackish-water animals. Many others should be mentioned also.

I must restrict myself here to a few special topics. I want to consider light especially because I believe it to be one of the most important factors in various biological processes in the sea. It is essential in plant assimilation for primary production in the oceans and therefore for productivity in general. Also animals are directly affected by light. Light permits them to orient themselves visually. Weak or normal light intensities often have a stimulating effect, as on muscle tonus, for example, but strong intensities may be inhibitory or even damaging. There are extreme gradients in illumination from the equator to the polar regions, from the surface to the depths, from the coasts out to the open sea. It varies regularly by day and also by season. These variations, depending on the time of day and on the season, are much more precise than temperature variations. Thus, some twenty years ago experimental work showed that the reproductive cycle of birds may be controlled by artificial illumination independent of temperature. Hence, the precision in the timing of bird migrations is apparently due to the regularity of the seasonal rhythm of light in the environment (Rowan, 1938). It should be noted that light is not a homogeneous factor, but that it includes several components: the total intensity, the various wavelengths of the spectrum, and polarization. Therefore it is interesting to outline the physiological-ecological effect of this factor in marine biology. In doing this, I shall restrict myself to certain problems of animal physiology since the relationship between plants and light will be discussed by other members of the Congress in connection with primary production.

It is a fascinating fact that the honeybee is dependent on polarized light in the sky in orienting itself when flying out to and returning from its food supply. It is also known (Waterman, 1950; Kerz, 1950; Burdon-Jones and Charles, 1958) that some littoral animals, such as *Limulus*, *Eupagurus*, and *Littorina*, can perceive polarized light. It is still not yet known whether polarized light is merely a directional factor. Indeed, it would be interesting to know to what depths littoral and oceanic animals can distinguish this sort of light. Furthermore, it is important to learn whether fishes can perceive polarized light and, if so, whether they orient themselves by it during their migrations.

The depths to which different animals can perceive light at all is an open question. Clarke (1936) took 750 m as a rough limit for a deep-sea fish, the eyes of which may be considered comparable to *Lepomis*. Waterman *et al.*, (1939) set 1500 m as the approximate depth for crustaceans. It is necessary to solve this problem not only by analogy but also by modern methods, for instance, by measuring the absorption of eye pigments under limited artificial conditions or by electro-physical measurements of the sensory cells. In different animals excitation of sensory cells are stimulated by very different light intensities. Hence, there will be very different maximal depths for the perception of sunlight or moonlight. Obviously, the spectral composition of the light must be considered in such work.

The problems of lunar periodicity are intimately connected with the perception of very weak light intensities or small variations in the light intensity. There are many periodic processes, such as moulting, migrations, for example in the silver eel (Lowe, 1952), and cycles of reproduction, the rhythms of which coincide with the phases of the moon. The discovery of these phenomena is a typical example of methods based on statistical comparisons. But it still remains to be explained whether biological rhythms are merely induced by variations in the intensity of the moonlight or whether there are other factors involved. In intensive laboratory experiments, Hauenschild (1955, 1956) investigated the lunar swarming in the polychaete *Platynereis dumerilii*. He was able to induce experimentally a new thirty-day rhythm with artificial light. Factors other than light were excluded and the dominance of light became evident during the course of his experiments. The minimal threshold for variations in the intensity of the light is 0.02 to 0.1 lux. This means that animals in their native benthic habitat must receive at least 0.02 to 0.1 lux more on nights of full moon than at the time of the new moon. The intensity of bright full moonlight at the surface is said to be about 0.5 lux. Certainly moonlight undergoes reflection from the sea surface and extinction with increasing depth below the surface in the same way as sunlight. Therefore one must postulate that intensities sufficiently high to exceed the threshold must reach benthic habitats. Consequently, we need exact data on the penetration of moonlight into sea water and we need physiological research on the sensitivity to very weak intensities of animals exhibiting various responses to lunar periodicity. There are many other questions concerning the special endogenous mechanisms for these rhythms, their hereditary character, and the external factors which determine them.

Many instances are known of animals having been damaged not only by ultraviolet light but also by visible light. Merker (1926) observed a strong interference with respiration in *Mysis* under strong illumination. Harvey (1929) recorded a decrease of about one-half from the normal in the frequency of the heart beat in the copepod *Calanus*, and Marshall *et al.* (1935) noticed a strong increase in the respiratory rate in this same organism on exposure to light. Plants are also known to be damaged by strong light: most diatoms occur at a depth of several meters below the surface. Many animals, especially in littoral habitats, prefer the dark or are active only at night, and remain hidden during the day. This too seems to indicate that they shun the light.

The physiological basis for this phenomenon still needs to be investigated. Probably strong light affects endocrine systems (Rasquin and Rosenbloom, 1954). Damage resulting from exposure to light can be increased markedly in the presence of fluorescent substances. The visible rays of these substances may be harmful to both animals and human beings. Such effects are widely known in medicine. In marine biology, on the other hand, only Pereira (1925) has reported such an effect. Eggs, sperm, and larvae of the sea urchin *Arbacia* are not injured by exposure to light in pure sea water or with the addition of eosin to cultures kept in the dark, but they soon die when exposed to light and eosin at the same time. Kalle (1949, 1951) demonstrated that sea water contains substances with a light blue fluorescence. Johnston (1955) confirmed this, and Koe *et al.* (1950) likewise isolated fluorescent substances from the sea bottom. The origin and chemical nature of these substances is not known, but it is supposed that they are derived from the metabolism and decomposition of organisms. It seems to be proved that the plant pigments phycoerythrin and fucoxanthin act as photosensitizers. Therefore, we may suppose that some pigments of pelagic diatoms or autotrophic flagellates are likewise fluorescent and may have an effect as sensitizers if in solution. There are two facts then: (1) the damaging effect of light on many animals in the sea and (2) the presence of fluorescent substances in sea water which in terrestrial habitats have a sensitizing effect. I am inclined to combine these facts to form the hypothesis that within the sea photodynamic effects are present which may play an important role in ecological relations. Naturally this hypothesis needs further confirmation. I think, however, that we can extend our understanding of such phenomena as, for example, under the heading "animal exclusion." The retarding or lethal effect of water from the English Channel on eggs and larvae of some polychaetes and echinoderms (Wilson, 1948–1954*) should be examined with this hypothesis in mind. It also seems desirable in connection with the antibiotic effect of plankton algae on bacteria (Steemann Nielsen, 1955). The hypothesis includes a means for understanding why *Calanus* sometimes occurs at the surface in bright sunshine, although it is generally very sensitive to light. Perhaps some bodies of water contain only a few fluorescent substances and therefore they will have very little photodynamic effect.

One of the basic ideas in this hypothesis is the combined effect of several environmental factors. Rabaud (1918) referred specifically to this problem. Moore and Kitching (1939) suggested that tolerance of any one factor by various organisms is greatest when all other factors are optimal. Some observations of marine animals indicate a relationship between light and temperature. Lewis (1959) pointed out that three species of copepods did not reveal any such relationship within their annual ranges of temperature in their natural habitat. However, above or below this range they shun stronger and weaker light intensities respectively. Dehorne (1918) stated that the syllid *Myrianida pinnigera* withstands temperatures up to 22°C in the dark, but it dies in light with only a small temperature rise. Moore (1950–1958) has referred on several occasions to the importance of the simultaneous action of light and temperature in vertical migrations of several zooplankters. In the speckled trout *Salvelinus fontinalis* Sullivan and Fisher (1954) found "that selection of temperature was apparently more precise at low intensities than at high intensities, although the actual temperature selected did not vary with a light intensity." From experiments, Hoar (1956) obtained a correlation in the goldfish between photoperiodicity and sensitivity to temperature. Finally, according to Marshall and Orr (1958) *Calanus* living at the same temperatures in August and February needs more oxygen in August. The authors suppose that different stages in development may provide an explanation. I think it possible that increased

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* For reference see Wilson and Armstrong (1958).

respiration in August depends on the stronger light intensity at that time. These examples stress the need for further research on the combined effects of light and temperature. Indeed, it will be desirable to compare animals from the eulittoral, sublittoral, and bathyal as well as those from equatorial and polar regions.

There is still another factor to be investigated in connection with light. From many ecological comparisons and experimental investigations we learn that penetration of marine organisms into brackish water depends on the temperature and oxygen content of the water (see references in Remane and Schlieper, 1958). Evidently this also depends on light, for many animals seem to prefer dark habitats on entering brackish or fresh water. I also wish to remind you of the numerous inhabitants of caves (see summary by Thienemann, 1950) and of coastal ground water. Remane and Schulz (1935) pointed out the eventual dependence on light. According to Sernow (1958), Brodski discovered Foraminifera living in springs of the Karakorum Desert in salinities of 5 to 11 ‰, whose nearest living relatives are found in the Mediterranean. The hydroid polyp *Cordylophora lacustris* prefers shady or dark places when living in fresh water (Roch, 1924). Kinne (1956, 1959) also has some interesting data on this animal. The amphipods *Talitrus* and *Orchestia* and their relatives live on beaches above the high water mark. They protect themselves against the light by burrowing into the sand. According to Rullier (1954) "l'abri est necessaire pour les tubes jeunes" of the brackish water polychaete *Mercierella*. Furthermore, the effect of light should be taken into consideration in the so-called brackish water submergency of Remane (1940, 1955, 1958).

Without doubt we can establish by statistical comparison a correlation between darkness or weak light intensities and the dilution of sea water. From this, we may deduce that penetration of marine organisms into dilute sea water is facilitated by the absence of light. This idea must be verified by experimental work. There is, however, one contradictory fact. Phototactic and phototropic reactions in some animals are affected by factors other than light, such as temperature, salt content, oxygen, or carbon dioxide.

In short, we have considered the following phenomena. (1) Light is one of the most important factors in primary productivity. (2) Light aids many animals by means of a visual orientation. Polarized light may have special significance in this connection. The importance of weak light intensities, especially in connection with lunar periodicity must also be taken into consideration. (3) Light often damages animals. A hypothesis is proposed that certain sensitizing substances may play a part in this. (4) Light and temperature seem to be correlated or interfere with one another. (5) Obviously tolerance to a decreased salt content is lessened in the light.

We should try to find a physiological interpretation for the last three points, but we do not have sufficient facts and must depend on mere suggestions of a rather theoretical nature. Provisionally I find this in the following considerations: Light as well as temperature and salt content affect an animal's respiration. In its normal habitat, the respiration rate is in part conditioned by temperature and in part by light. Respiration has two chief components: (1) internal respiration within the cells and (2) the exchange of gas between an animal and its environment. These must be in balance. It will shift in the same direction with a rise in temperature and with increasing light. Therefore, in order for respiration to continue within its optimal range, an animal must avoid light with a rise in temperature and vice versa. In Fig. 1, the crosses

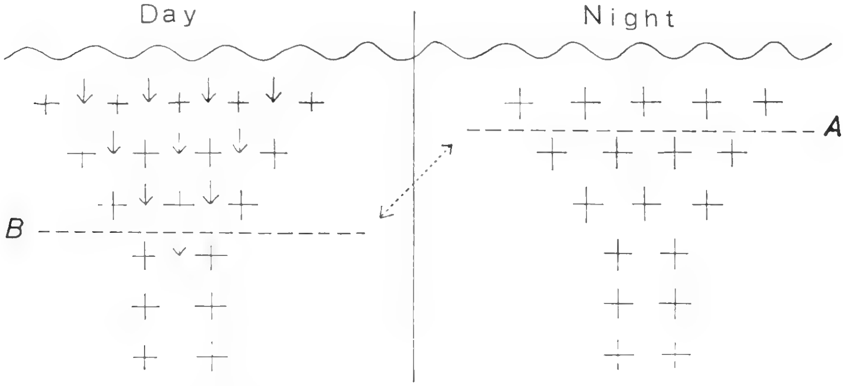

Fig. 1. The combined effect of light and temperature on the vertical distribution of zooplankton (schematically).

indicate arbitrary units of temperature-conditioned respiration. If we assume that the optimal respiration rate is reached at a level of five such units, then the animal will live near the surface during darkness (A). By increasing the light, there will be an increase in respiration say by four arbitrary units. Total respiration would then rise to 9 units which far exceeds the optimum. Animals will then leave the surface zone and descend to a level where respiration is again at an optimum of five units conditioned by light and temperature together (B). It is stressed that this is merely a tentative idea and needs further investigation. Furthermore, there may be other factors which influence respiration, as for example, the quality and quantity of food or metabolic substances in the environment derived from other animals and plants.

An increase in temperature and light intensity as well as dilution of sea water will cause an increase in respiration. That does not necessarily mean that the mechanism for a reaction is the same in all organisms. A rise in temperature induces an increase in the entire metabolism; fluctuations in salt content cause a change in the state of hydration of the protoplasm and releases osmoregulatory processes; the effect of light may be found in its effect on any endocrine system. These questions must be investigated. It should be noted that the two sexes may react quite differently as may the various developmental stages. In addition, there may be some adaptations which differ in their reactions in the field and in the laboratory.

Finally, two other phenomena must be mentioned in connection with the climate of light in the sea. There are vitamins whose synthesis is dependent on light. Thus, none of them can be produced at great depths. Deep-sea animals may suffer for their lack or get their supply in a roundabout way. The cartilaginous nature of the skeleton in deep-sea fishes, for instance, is said to be due to an avitaminosis. In this connection, the following points must be considered. (1) According to Fisher (Fisher *et al.*, 1955; Fisher and Goldie, 1959), the Euphausiacea are especially rich in carotenoids and in vitamin A. These animals undergo extensive vertical migrations and serve as the principal source of food for other animals at greater depths. Thus, vitamins are transported through migrations of this sort down to such depths. (2) Very recent investigations indicate that there is a great variety of heterotrophic plants in the aphotic zones of the oceans: bacteria, yeasts, fungi, and flagellates (ZoBell, 1946; Kriss, 1959; Höhnk, 1952–1956; 1959). What about their ability to synthesize vitamins? We do not know. Perhaps they are autochthonous producers in the deep sea. (3) In connection with the cartilaginous nature of skeletons of deep-sea animals it must not be forgotten that physicochemical conditions in deep water are quite different from those near the surface. For example, Wattenberg in the 1930's (1933; 1936) reported that dissociation of carbonic acid is increased by hydrostatic pressure and that therefore the solubility of calcium carbonate is increased. This means that deposition of calcium carbonate by organisms is greatly reduced.

The second phenomenon to be mentioned is the part light plays in the radiation "climate." Its importance in evolution is quite another chapter in marine biology.

Summarizing, we see that illumination beneath the sea surface by light from both the sun and moon is extremely important in various biological phenomena in its intensity, in its spectral composition, its effect in combination with other factors such as temperature, the salt content or fluorescent substances, and its role in productivity, in the synthesis of vitamins, and finally in evolution. One must conclude that our knowledge of light in the sea must be increased markedly in order to analyze and to understand a great many different biological processes in the sea. It provides a wide field for cooperation between physicists, chemists, and biologists, as is true in many other problems in oceanography.

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Cultivation of Marine Organisms as a Means of Understanding Environmental Influences on Populations

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AT a symposium on "Perspectives in Marine Biology" a few years ago the distinguished oceanographer Dr. Alfred C. Redfield gave a paper with the rather provocative title: "On the inadequacy of experiments in marine biology" (Redfield, 1958). Although admitting the great value of contributions from physiologists, Redfield concluded that "the greater need at the moment is more knowledge of the phenomena to be explained." One can follow Redfield a long way in his argument for intensifying the study of conditions in the sea in order to obtain a more precise description of the qualitative and quantitative distribution of populations as related to environmental factors. However, marine biologists working on field ecological studies may not in general wholeheartedly agree with his conclusion. It may not be wrong to say that there is a general feeling among marine ecologists that precisely the combination of field work and laboratory experiments is essential to progress in the biological field of oceanography. Another question is whether this feeling is sustained by the results, which have so far been achieved through experiments. The general title of this paper is so wide that it will be necessary to illustrate the experimental approach with the use of cultures by examples and these have been chosen from my own field of marine phytoplankton. I would like to make it clear that I have chosen to abstain from dealing with the more general studies of, say, plant physiology, which undoubtedly are of the greatest value for the study of marine phytoplankton in general. In this way the scope of the following discussion will mainly be a consideration of experiments dealing with specific differences among the members of the marine phytoplankton in their reaction to the environment.

Field observations have revealed a variety of patterns in horizontal and vertical distribution, and pronounced annual cycles of species, leading to a succession of plankton societies. It is characteristic of the marine phytoplankton that the details in this succession may change from year to year in the same habitat. An analysis of these striking events requires knowledge of the reaction of each species or group of species to the environmental conditions.

The reason for my taking this opportunity to review the autecological aspect especially is not that there are many spectacular results to present. On the contrary, the scarcity of available experimental data forces me to stress mainly the need for an intensification of effort, in order to establish a harmonic progress in the study of the producers in the sea.

Let us first review briefly what information studies on cultures have afforded as to the influence upon various marine phytoplankton species of such environmental factors as salinity, temperature, light, and inorganic nutrients, which are subject to routine recording in oceanographic investigations. Salinity and temperature are generally accepted as important for the distribution of species, while light and inorganic nutrients are recognized as controlling factors for growth of the population in general. As the first of these classical ecological factors we may consider salinity.

Salinity

For the diatoms, which form such an important part of the planktonic vegetation, even in tropical waters (Hasle, 1959), the only records on how salinity affects growth are from Kain and Fogg's (1958) experiments on *Asterionella japonica* (Fig. 1). They indicate an optimum at a salinity of 30‰ and no growth at 15‰ and below. In Danish waters, with a wide range in salinity, the

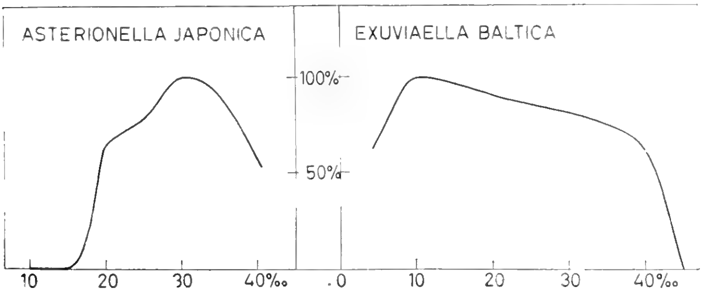

Fig. 1. Growth at different salinities as percentage of maximal growth rate (Kain and Fogg, 1958; Braarud, 1951).

samples with *Asterionella* showed a mean of 31.5‰ (Ostenfeld, 1913) and, likewise, its general occurrence in the Atlantic and the Mediterranean at salinities above 35‰ and its absence in brackish waters accord well with the experimental findings.

Cultures of dinoflagellates isolated from the Oslofjord show somewhat different curves for the salinity effect upon growth. Let us first consider *Exuviaella baltica* (Fig. 1). The growth rate is remarkably high within the whole range from 10‰ to 40‰, with a slight indication of an optimum around 10‰. These results are in agreement with field records of its abundant occurrence in waters of widely different character. It occurs in the brackish waters of the Baltic, in the waters of varied salinity around Denmark, in the North Sea and the coastal waters along Norway, in the oceanic parts of the Norwegian Sea and the North Atlantic, in the Barents Sea, and even in polar waters along the east coast of Greenland. Obviously salinity does not restrict its distribution, except in marine waters of extremely low salinities.

If we consider the other dinoflagellates from the Oslofjord area (Fig. 2), we may first point out that, like *Exuviaella baltica*, these also have optima at salinities below 30‰, namely between 15‰ and 20‰, values which coincide with those for the surface waters in the Oslofjord in summer, when these species occur in greatest abundance. The main difference between the species is found in their response to low salinities.

Peridinium triquetrum, is characterized by fairly good growth

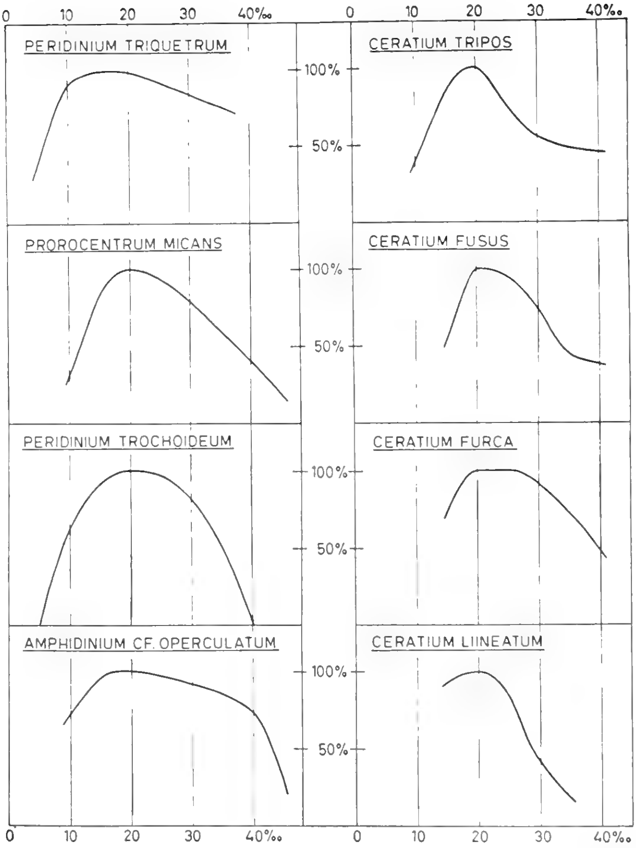

Fig. 2. Dinoflagellates: growth at different salinities, as percentage of maximal growth rate (Braarud 1951; Braarud and Rossavik, 1951; Nordli, 1957).

even at 5‰ (Braarud and Pappas, 1951). This explains how this species is able to thrive as far into the Baltic as in the harbor of Helsingfors, where the salinity, according to Välikangas (1926), may vary between 3.5‰ and 6‰. The *Ceratium* species also show differences in this respect, *C. tripos* being the only one in Nordli's experiments (1957) which reproduced at 10‰ (Fig. 2). This species is known to penetrate farther into the Baltic than the other species of this genus, although it does not go as far in as *Peridinium triquetrum*. This feature in its distribution finds a reasonable explanation in the response observed in the salinity experiments.

For the dinoflagellate species *Exuviaella baltica, Peridinium triquetrum,* and *Ceratium tripos,* the salinity experiments have thus given an explanation of characteristic features in their distribution in habitats of relatively low salinity. In the other species investigated, there is an overall agreement between the results obtained in the experiments and the known distribution of the species. This fact indicates that experiments on clone cultures from one locality may give results which are applicable to the population of the species within a larger area.

Beforehand one might have reason to doubt whether this would be the case. In experimental work of this kind one may question whether clones or strains are constant in their response to environmental conditions; whether a single clone is representative of a local population, and one may even ask if there exist geographical races, especially in species with a very wide distribution. Only a very few observations are available for elucidating these points, which are of obvious importance when trying to apply experimental results to the understanding of what happens in the sea.

In Fig. 3 are shown graphs from salinity experiments on the same clone of *Peridinium trochoideum* at different temperature conditions and with media made up of different batches of sea water. It will be seen that the general features of these curves are similar: an optimum appearing at about 20‰, while reproduction at higher salinities differs somewhat. Two clones of *Prorocentrum micans,* both from the Oslofjord, but isolated at different times, also show

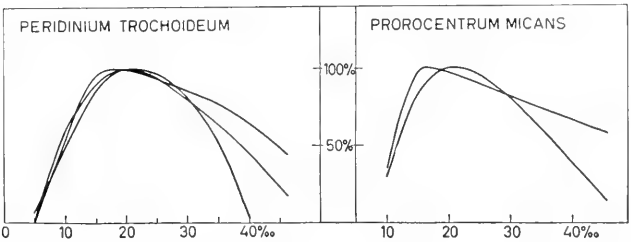

Fig. 3. Growth at different salinities as percentage of maximal growth rate. *Left,* experiments on the same strain from Oslofjord; *right,* experiments on Oslofjord strains from different years (Braarud, 1951).

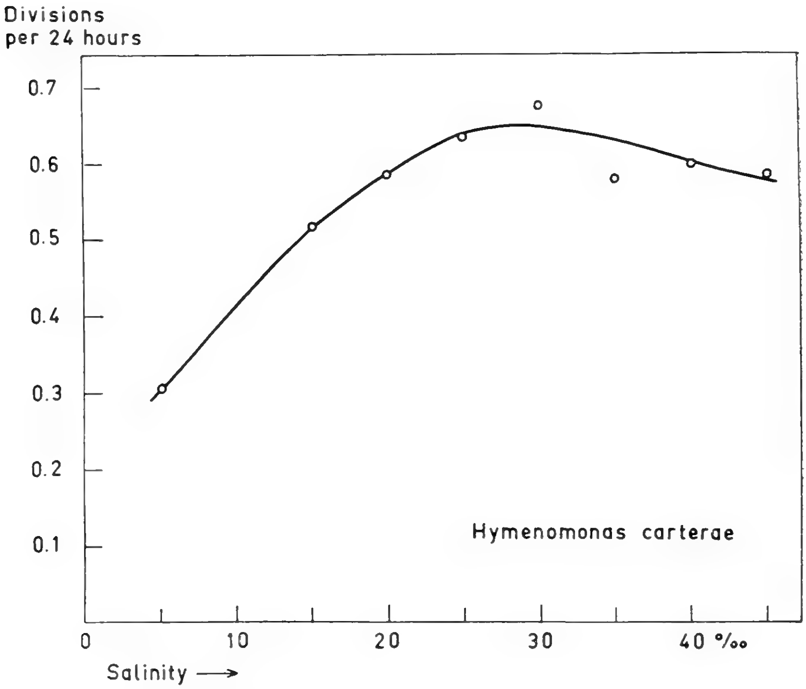

Fig. 4. *Hymenomonas carterae*: growth rate at different salinities (Braarud, 1951).

essentially similar features in their response to salinity: Low growth rates at 10‰ and a quick rise to 15–20‰, with a slow decline when salinity rises to 40‰.

For clones of the same species originating in widely separated localities, there is one observation, again of *Peridinium trochoideum*. The salinity-growth relationship has been studied in clones from the Oslofjord, where the salinity during its abundant occurrence in summer is about 20‰, and from Golfo di Napoli, where salinity is as high as 37‰. These clones gave practically identical curves with an optimum of salinity as low as 20‰. These last results indicate a uniform salinity response in populations inhabiting waters with widely different salinity conditions, thus giving no hint of geographical races in this species, which has a worldwide distribution.

Turning now to the third important group in the marine phytoplankton, the coccolithophorids, there are only two species whose salinity-growth relationship has been studied: *Hymenomonas carterae*, originally referred to *Syracosphaera* (Braarud, 1951), and *Coccolithus huxleyi* (Mjaaland, 1956). *Hymenomonas carterae* is, as far as we know, an inshore species. The clone used in the experiments was isolated from an artificial oyster pond where the salinity during its occurrence varied between 17‰ and 30‰. In culture it showed very good growth between 15‰ and 45‰, but even at 5‰, growth was fair (Fig. 4). Obviously salinity is not an important environmental factor for this species, which has only been observed in abundance in littoral pools (Carter, 1938; Braarud and Fagerland, 1946) where salinity is apt to show great variation.

The other coccolithophorid, *Coccolithus huxleyi*, showed good growth between 20‰ and 45‰, while it was also able to grow at 15‰ (Fig. 5). This is in accordance with its worldwide distribution in oceanic waters of salinities around 35‰ and in coastal waters of northern Europe as well, where it may occur in extremely dense populations at lower salinities of between 15‰ and 20‰ (Lohmann, 1908; Birkenes and Braarud, 1952). The experimental results indicate that it requires too high a salinity to be able to populate truly brackish waters.

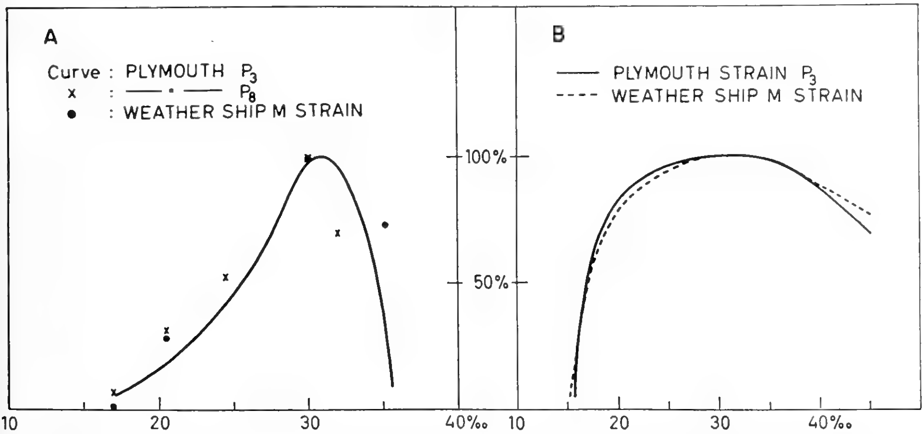

Fig. 5. Growth of *Coccolithus huxleyi* at different temperatures (A) and salinities (B) as percentage of maximal growth rate (Mjaaland, 1956).

Looking back upon these scattered observations of growth response in marine phytoplankton to the salinity of the environment, it may be stated that, so far as these go, they justify confidence that information from experimental results may be applied successfully in interpreting records from surveys at sea. The consistent results for different clones of dinoflagellates from the same locality, or from widely separated localities, indicate that even with the use of a clone from only one locality, the results may be applied for populations of a large area. However, when we turn to the temperature experiments, we soon see that the picture is more confused.

Temperature

Since the first biogeographical surveys of marine phytoplankton, temperature has been regarded as an essential ecological factor for the geographical distribution of each species. Terms such as arctic, boreal, temperate, and tropical species are generally used with the implication of a decisive temperature effect upon growth and survival. In trying to explain the succession of diatom species in north European coastal waters during the spring maximum and the following decline, temperature has also been suggested as an important factor. Attempts at verifying the validity of these assumptions through experiments are, however, few.

In Table I data have been gathered from field observations and from experiments for the few planktonic diatoms which have been studied as to the effect of temperature upon growth. Schreiber

TABLE I. Temperature-Growth Relationship in Marine Plankton Diatoms[a]

Species	Temperature during Periods of Abundance	Optimal Temperature in Culture
Biddulphia aurita	1°C	(5°C)
Biddulphia sinensis	13°C	(16°C)
Asterionella japonica	8°C (Gran)	20–25°C
	Above 20°C (Danish invest.)	
Thalassiosira nordenskioeldi	2–3°C	Excellent growth at 10–11°C

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[a] According to Ostenfeld, 1913; Schreiber, 1927; Gran, 1929; Braarud, 1937; Grøntved; 1949.

(1927) found that the winter species *Biddulphia aurita* showed far better growth at low temperature than at ordinary room temperature, whereas the summer species *Biddulphia sinensis* reproduced slowly at 5° and 9°C, but showed good growth at 16°C. Schreiber concluded that this difference in temperature response gives an explanation of the different seasonal occurrence of the two *Biddulphia* species in the North Sea.

On the other hand, recent experiments on *Asterionella japonica* by Kain and Fogg (1958) gave results which are at variance with those obtained by some of the field observations. Gran (1929) reviewed the available field observations and concluded that *Asterionella*, judged from its distribution, has a temperature optimum at about 8°C, and that it is also abundant in waters of lower temperature, a conclusion which was supported by subsequent records from the North Sea area by Braarud *et al.* (1953). Kain and Fogg (1958) observed, however, a definite temperature optimum at 20–25°C and no growth below 10°C in a nonbacteria-free culture (Fig. 6). The picture is becoming still more complicated by the observations from Danish inshore waters by Grøntved (1949) demonstrating abundant occurrence of *Asterionella* at a temperature of 20–25°C. It becomes evident that neither the conclusions drawn from field observations by Gran (1929) nor the experimental results by Kain and Fogg (1958) provide an adequate characterization of the temperature response of *Asterionella*.

Another discordance between the sea temperature during periods of abundant occurrence and its growth in culture was observed by Braarud (1937) for *Thalassiosira nordenskioeldi*, a boreal neritic diatom species which also occurs in polar waters. Ostenfeld (1913) gives a mean temperature for its occurrence in Danish waters of about 2°C, a temperature which is similar to that found by Gran and Braarud (1935) for waters showing the greatest abundance of this species in the Fundy region and likewise, by Ramsfjell (1954) and Paasche (1959) for the Norwegian Sea. In culture, however, Braarud found that it showed excellent growth also at a temperature as high as 10–12°C, with growth rates which presumably are near to the maximal ones for the species.

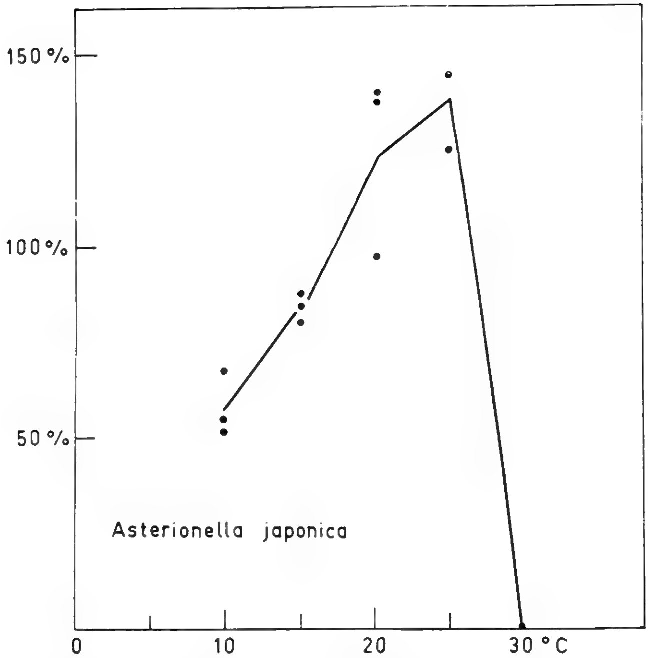

Fig. 6. *Asterionella japonica*: Growth at different temperatures as percentage of controls (Kain and Fogg, 1958).

Before discussing how the results for *Asterionella japonica* and *Thalassiosira nordenskioeldi* may be interpreted, we may look at observations of representatives for the two other main groups.

For dinoflagellates the growth-temperature relationship of a number of species has been studied in nonbacteria-free strains from the Oslofjord. The results are presented in Fig. 7. In all these cultures optimum was observed in the region of 15–20°C, which is the temperature range for summer, when these species, with the exception of *C. lineatum*, are found in greatest abundance. *Ceratium lineatum*, which Nordli (1957) in his experiments found to have an optimum at 20°C also, has its main occurrence in the Oslofjord at seasons when the temperature is lower. This species shows, however, good growth at lower temperatures as well and other ecological factors, such as the nutrient supply, may be responsible for its prevalence in seasons other than summer. The

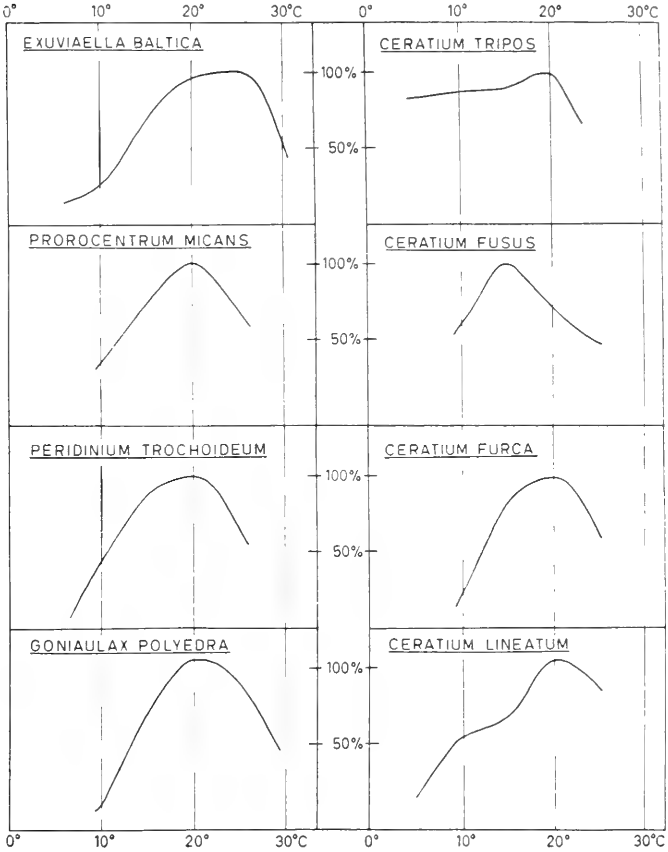

Fig. 7. Dinoflagellates: growth at different temperatures as percentage of maximal growth rate (Bakken, unpublished; Nordli, 1957).

relatively high growth rate of *Ceratium tripos* at low temperatures, as compared with the other ceratia studied by Nordli, gives a reasonable explanation of the predominance of this species in the cold season in the Oslofjord area, as compared with other species of the genus such as *Ceratium furca* and *fusus*.

In recent experiments on a strain of *Peridinium trochoideum* from Golfo di Napoli, the temperature optimum was found to be as high as 25–30°C (Fig. 8), while the Oslofjord strain showed an optimum at 20°C as did the other dinoflagellates from the Oslofjord area (Fig. 7).

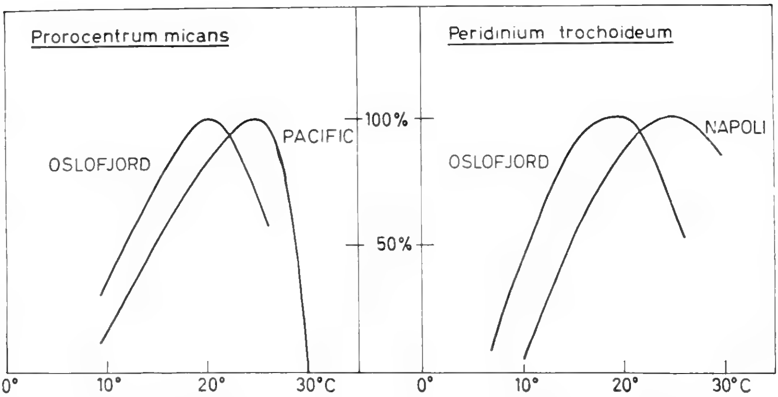

Fig. 8. Temperature response in strains from different geographical regions (*left*, Barker, 1935, and Bakken, unpublished; *right*, Bakken, unpublished, and Braarud, unpublished).

A similar displacement of the optimum is known from temperature experiments on *Prorocentrum micans*. The Oslofjord strain of this species showed a definite optimum at 20°C, whereas Barker (1935) in experiments with cultures from the coast of California observed an optimum at 25°C (Fig. 7).

In the coccolithophorid *Coccolithus huxleyi* Mjaaland (1956) observed a temperature optimum at about 20°C and growth at as low a temperature as 7°C (Fig. 5). This reaction is in fair agreement with observations from surveys, although these indicate that growth may even take place at a considerably lower temperature.

For the available temperature experiments the comparison with field observations gives a less coherent picture than the salinity experiments. There are examples of a general agreement between the experimental results and the field data, as for the dinoflagellates from the Oslofjord, and there are instances of pronounced disagreement as for *Asterionella japonica* and *Thalassiosira nordenskioeldi*. Two explanations may be suggested for these discrepancies and both may be involved: that the experimental technique has been unsatisfactory and given erratic results, or, that the deductions from biogeographical data are erroneous and have blurred the ecological picture for the species in question, as suggested by Braarud (1937) in the case of *Thalassiosira nordenskioeldi.*

The main objection to the technique used may be that the cultures were not bacteria-free. In such a case two effects may be responsible for the different growth rates of a culture at different temperatures: (1) the response of the alga to the temperature factor, the response which we are looking for, and (2) the response of the bacterial population in the culture which may, indirectly, influence the rate of growth of the algal population. As long as we have no parallel temperature experiments with and without bacteria as associates, we are unable to judge how important the latter effect may be, but the recent discovery of the vitamin requirements of the plankton algae lends some support to such a view. It would not seem unreasonable to suggest that the difference between the temperature optima observed in the experiments with strains of *Peridinium trochoideum* and *Prorocentrum micans* from widely separated localities might be due to the difference in the bacterial populations of the two cultures, since the latter may presumably provide vitamins necessary for growth.

The other alternative, that temperature is not a decisive environmental factor for the abundance of a species such as *Thalassiosira nordenskioeldi* at low temperature and its absence at higher temperature, as indicated by the experiments, finds some support in the fact that the rise in temperature in spring in northern Atlantic waters coincides with a decline in the supply of inorganic nutrients. Species demanding fairly high concentration of nutrients, therefore, might show a similar seasonal occurrence as a cold water species. Only new experiments with bacteria-free cultures can give us a clearer picture of the actual temperature effect upon growth.

From the experiments on the salinity and temperature factors it may be concluded that the tolerance of the various species to extreme conditions should be studied with special care.

The two remaining environmental factors of this group, light and nutrient supply, can be dealt with quickly as very few observations are available for a discussion of specific differences. Photosynthesis experiments with cultures of diatoms suspended at different depths were carried out by Marshall and Orr (1928) and by Jenkin (1937). These classic investigations demonstrated clearly the important feature that, in the diatoms which they used in their experiments, an inhibition of photosynthesis occurred near the surface, the depth for the photosynthesis optimum varying according to time of day and season. Marshall and Orr found that the winter species *Coscinosira polychorda* and a summer species of *Chaetoceros* had the same optimum light intensity but that inhibition at the surface was more pronounced in the *Chaetoceros* species. The latter result was unexpected, and the authors suggest that it might be due to the fact that the *Chaetoceros* species had been grown in weak light. Jenkin worked on the diatom *Coscinodiscus excentricus* and to a lesser extent on *Biddulphia regia*, which are both winter forms. They were found to have similar optimum light intensities.

Jenkin concluded that the greatest scope for future work would seem to lie in the laboratory, but during the twenty years which have elapsed since her paper was published, only incidental observations of this kind have been made. Mjaaland (1956) observed excellent growth in the coccolithophorid *Coccolithus huxleyi* even at as strong light as 50,000 lux while Nordli (1957) in his experiments on ceratia, observed an optimum between 2,500 and 5,000 lux. He concluded that his results were at variance with the vertical distribution pattern of these species. Lanskaja and Sivkov (1950), who studied growth of five diatoms, remark that there is reason to believe that photosynthesis and also growth may differ according to the state of the cells and their previous history, a view also held by Marshall and Orr (1928). This is in accordance with the behavior of other algae, and may explain the extremely low optimum intensities observed by Schreiber (1927) in the case of the two species of *Biddulphia*.

The general effect of light upon phytoplankton photosynthesis and growth seems to be well established by studies reviewed by Steemann Nielsen (1958b), and by Steemann Nielsen and Jensen (1957), but it is obvious that too few investigations of the light response of the various species are available for a comparison with their distribution in the sea. Field observations indicate that in this respect also we may find important specific differences, but much basic work is required in order to obtain a satisfactory method for further studies.

The possibility of different responses to varying concentrations of inorganic nutrients was brought into the spotlight by Rodhe (1948) through his observations of extremely low maximal values for various freshwater species. For the truly marine forms experiments are not available to judge whether this ecological factor is responsible for exceptional distribution patterns in certain species. So far, the experimental approach in studying the environmental influences on marine phytoplankton has been for orientation purposes. In future special attention should be paid also to the interaction of the various factors.

The technique of the experiments has been simple. The cultures have not been bacteria-free. The media have been enriched sea waters, with or without soil extract as a supplement, and consequently not well defined. As long as this was the case, problems of more special nutritional requirements could not be approached. These defects have been obvious to workers in the field and may be partly responsible for the restricted nature of the activities.

Since the pioneer research on cultures of marine phytoplankton initiated by Miquel (1890–93) and especially by Allen in Plymouth more than half a century ago, a great number of attempts have been made to introduce synthetic media by using artificial sea water. Allen himself, partly in collaboration with Nelson, made experiments of this kind (Allen and Nelson, 1910; Allen, 1914) and made the important observation that only with the addition of small amounts of natural sea water could satisfactory growth be obtained. Subsequent work proved that in most cases growth in artificial sea water was not as good as in Allen or Schreiber sea water with soil extract, or that no growth at all took place. The importance of the organic components of natural sea water for diatom growth was demonstrated by Harvey (1939), but it was not till the general occurrence of auxotrophy in marine phytoplankton had been discovered that the basis was laid for introducing well-defined media of a satisfactory composition. Through the contributions by Provasoli, Hutner, and their collaborators in

New York, by Droop in Millport, and Sweeney at La Jolla (for literature, see Droop, 1957) information has been obtained on the vitamin requirements of representatives for marine diatoms, dinoflagellates, and chrysophyceans, especially as to vitamin B_1 and B_{12}. These results have been reached by means of an improved technique which we shall consider before presenting some of the findings of their research into the necessity of organic compounds for growth.

The new technique is the result mainly of the work by Provasoli and his collaborators (see Provasoli *et al.*, 1957) on the composition of media, and of the success of various workers in establishing bacteria-free cultures. Compared with the older synthetic media the new ones are characterized by the following improvements: (1) a uniform and satisfactory supply of micronutrients by means of chelating agents as EDTA (ethylenediamine tetraacetic acid), (2) buffering of the medium by means of a compound which is not used during the growth of the alga, as TRIS (hydroxymethylaminomethane), and (3) addition of defined quantities of organic compounds required by the alga, as vitamin B_1 and B_{12}, which were previously supplied by the natural sea water and the soil extract (Sweeney, 1954).

The use of these compounds has made it possible not only to obtain satisfactory growth in synthetic media with a general composition similar to that of sea water but also to make essential changes in the ionic composition of the medium for a study of the relative importance of the various components of sea water, as made by Provasoli *et al.* (1954). Droop (1958b) has used this technique in a study of euryhaline species from littoral pools and of the pelagic diatom *Sceletonema costatum* and has drawn the tentative conclusion that the different salinity response of the various species is due mainly to their special requirements for the concentration of sodium ions in the medium.

One of the main drawbacks with the Allen technique was the presence of bacteria and colorless flagellates in the persistent cultures. Schreiber (1927) devised a special apparatus for washing diatoms in order to get rid of bacteria. Jenkin (1937) used a treatment with iodine, suggested by Allen, for destroying at least the major part of the bacterial population, but did not obtain truly pure cultures. During recent years bacteria-free cultures of several species of marine diatoms and flagellates have been obtained. Two methods have been used: (1) simple washing with sterile medium and (2) treatment with antibiotics, with minor variations in the procedure (for literature, see Spencer, 1952; Droop, 1954). If these methods are combined with the use of a varied selection of media, there should now, as indicated by Droop, be a far greater chance of success in establishing bacteria-free cultures of the autotrophic members of the marine plankton, although obstacles may still be encountered (Kain and Fogg, 1958). Special efforts ought to be made to improve still further the isolation technique.

We may now return to the results which have been obtained by the use of this new technique. Droop (1957) has summarized the results on the vitamin requirement of marine phytoplankton species up to 1957. Table II shows that the four chrysophyceans which were studied in bacteria-free cultures have the same requirements for vitamin B_1 and B_{12}, while the two diatoms, *Phaeodactylum tricornutum* and *Sceletonema costatum*, differ. *Phaeodactylum* requires neither of them, whereas *Sceletonema*

TABLE II. Vitamin Requirements in Bacteria-Free Cultures (Droop, 1958a)

	B_{12}	Thiamine	Portion of Thiamine Required
Chrysophyceans			
Monochrysis lutheri	+	+	Pyrimidine
Prymnesium parva	+	+	
Syracosphaera elongata	+	+	
Microglena arenicola	+	+	
Diatoms			
Phaeodactylum tricornutum	—	—	
Sceletonema costatum	+	—	
Dinoflagellates			
Oxyrrhis marina	+	+?	Thiazole
Glenodinium foliaceum	+	—	
Peridinium trochoideum	+	—	

requires B_{12}. One of the dinoflagellates, the nonphotosynthetic *Oxyrrhis marina*, requires both, whereas the two photosynthetic species probably have no need for B_1 in the medium. The chrysophyceans require the pyrimidine component of thiamine, while the dinoflagellate *Oxyrrhis* uses the thiazole component.

The possible ecological implications of these results we shall leave for a brief consideration later, but there is another principal feature which may be stressed here. Although only a few representatives of the various taxonomic groups have been investigated, the results indicate a diversity in the requirements of various species within the same taxonomic group, as shown for the diatoms and the dinoflagellates. This is still more clearly demonstrated by the response to various compounds of the B_{12} group as presented by Provasoli (1958). As will be seen from Table III, there are in chrysomonads and in dinoflagellates differences as to their ability to utilize the various cobalamins, two types being represented among the chrysomonads and two within the dinoflagellates, while the diatoms add to this diversity.

These results make it evident that generalizations of results obtained for this feature of the metabolic pattern, would be unwarranted. They may also be taken as a sign that great variations may occur not only in this aspect but also in the general response of the various species of a taxonomic group to the composition of the medium and other environmental factors. This was also indicated by the experiments on the salinity factor which have been referred to previously. What the situation will be if we consider ecological groups, established by field observations, is a question that cannot be answered until more species have been examined.

Provasoli and Pintner (1953), Provasoli (1958), and Droop (1957) have discussed the possible importance of the auxotrophic demands of the various species for their occurrence in the sea. Undoubtedly interesting ecological implications suggest themselves while the available information on the occurrence of vitamins in the sea continues to be rather scanty (Cowley, 1956), so it would seem premature to draw definite conclusions. The work on vitamin requirements is, however, of paramount importance for experimental studies on cultures. In addition to the other im-

TABLE III. Specificity of Marine Organisms toward Cobalamins (Provasoli, 1958)

Organisms	B_{12} (5,6-dimethylbenzimidazole)	5,6-Dichlorobenzimidazole analog	Benzimidazole analog	B_{12} III (Factor I)	Factor A (2-Methyladenine)	Factor H (2-Methylhypoxanthine)	Pseudo B_{12} (Adenine)	Factor B (No Nucleotide)
Chrysomonads								
Prymnesium parvum	+	+	+	+	○	○	○	○
Microglena arenicola	+	+	+	+	○	○	○	○
Syracosphaera elongata	+	+	+	+	○	○	○	○
Isochrysis galbana	+	+	+	+	○	○	○	○
Monochrysis lutherii	+	+	+	+	+	+	+	○
Dinoflagellates								
Gyrodinium californicum	+	+	+	+	○	○	○	○
Gyrodinium resplendens	+	+	+	+	○	○	○	○
Gyrodinium uncatenum	+	+	+	+	○	○	○	○
Amphidinium klebsii	+	+	+	+	+	+	○	○
Amphidinium rhynchocephalum	+	+	+	+	+	+	○	○
Diatoms								
Skeletonema costatum	+				+		+	+
Amphora perpusilla	+	+	+	+	+	+	+	+

Note. + = active; ○ = inactive.

provements of the media, the knowledge of the need for these organic compounds and the success with the isolation of bacteria-free cultures seem to promise that a new era has been initiated in experimental studies of the autecology of the marine phytoplankton.

There are also other indications that a more satisfactory basis for such work can now be established. I refer to recent work on the life cycle of the plankton algae. The species, which would be most suitable for culture work and studies on the influence of environmental conditions on their occurrence, are those which reproduce by binary fission, without any complications in the form of sexual reproduction or cyst formation. Among the more important groups of plankton algae, the dinoflagellates seem to be closest to this ideal. None of the marine brown dinoflagellates which have been cultured, representing species of *Amphidinium*, *Ceratium*, *Exuviaella*, *Goniaulax*, *Gymnodinium*, *Gyrodinium*, *Peridinium*, *Prorocentrum*, and *Protoceratium*, has shown any sign of sexual reproduction. Some of them form cycts when the cultures become too dense or old, but there are no difficulties in keeping the cultures in active growth without cyst formation.

The diatoms, on the other hand, are not so easily handled in culture work. Their special mode of cell division, whereby one of the daughter cells becomes smaller than the other, leads to a variation in cell size within a population. Transitions from narrow to broad cells take place through auxospores, in connection with sexual reproduction. In species where auxospore formation takes place readily, the average cell size may not vary excessively, while in other species, which form auxospores at longer intervals, populations with very different values for the average cell size may occur both in nature and in culture. As the growth rate is likely to vary with cell size, more extensive experiments must be carried out in order to obtain results which are applicable for interpretation of field observations. For the culture work an intimate knowledge of the life cycle of the species in question and the conditions of sexual reproduction are therefore of great value. Through the work of von Stosch (1954) the methods for life cycle studies on centric diatoms, which are predominant in the sea, have been demonstrated, and this field calls for experimental work on a large scale. Field observations indicate that there is considerable variation between the species as to the frequency of auxospore formation. Detailed information on this point, required for a satisfactory handling of diatom cultures in autecological work, can be obtained only through laboratory experiments.

The third large group of plankton algae, the coccolithophorids, has also, one may say rather unexpectedly, disclosed a complicated life cycle. In *Coccolithus fragilis* Bernard (1939) has suggested a tentative life cycle, which includes the regular occurrence of palmella stages in the sea. Quite recently Parke (1959) has been able to show experimentally that the species *Crystallolithus hyalinus* represents the motile stage of the well-known *Coccolithus pelagicus*, which, according to Parke, has the character of a cyst. This is an observation which gives quite a new viewpoint to the understanding of distribution related to environment in these forms. Observations on *Coccolithus huxleyi*, the commonest of all marine coccolithophorids, indicate that problems are also in store concerning the life cycle of this species.

This type of experimental work has been dealt with so extensively here because it is essential both in direct interpretation of the observations from the sea and in the introduction of a technique whereby uniform material for culture work may be obtained. The recent achievements give promise of obtaining very important information through continued studies within this field.

Looking back upon the work which has been done on cultures of marine phytoplankton, we notice that the experimental results have been related to only a few of the many problems facing a field ecologist. For many reasons it was natural to start with environmental factors such as salinity and temperature, which had been used so extensively for interpretation of specific differences in distribution. A basic knowledge of the influences of these factors would also seem to be a prerequisite for a closer study of the finer details in distribution pattern and seasonal occurrence.

As activities have been so restricted and, unfortunately, a great part of the experimental work has been made on species which are not observed regularly in the sea, such as *Phaeodactylum* *tricornutum,* the former *Nitzschia closterium* f. *minutissima,* there is a host of unsolved problems calling for studies by means of experiments with the use of cultures. The mention of a few problems may be allowed.

The annual cycle of the phytoplankton, which has such characteristic features in higher latitudes, has been investigated in all-year surveys and, in many cases, the general trend has been found to relate well with changes in the supply of nutrients, stability conditions, and light supply, but we cannot yet give any substantiated explanation of the succession of species. Several theories have been advanced, but these have a common lack of background knowledge regarding the actual behavior of the organisms in question. We have already seen how doubtful the information is on the temperature response on the few species which have been studied. The situation is no better in the case of the mutual effect of species growing together, for instance by means of ectocrine substances. This factor has been suggested as playing a part in producing succession, but this has still to be proved. The different rate of growth in the various members of a society is obviously of prime importance for their relative abundance, but actual knowledge of the rate of reproduction in diatoms, dinoflagellates, and coccolithophorids is so fragmentary that it cannot be used for estimating with any certainty the effect of this feature in individual cases.

Extreme mass occurrence of certain species, as for instance in red tides, represents an interesting and spectacular example of societies presumably resulting from hitherto obscure conditions favoring growth in certain species. These are normally members of societies of a more balanced composition.

Form variation is observed in every species. In some cases there seems to be a phenotypic variation which has been tentatively related to the influence of temperature, salinity, nutrient salt concentration, and day length. Experimentally little has been done in this field. For Ceratia, Nordli (1957) observed variation in size with changes in temperature and, in the case of rather abnormal forms, he found their occurrence to be related to an ample supply of nutrients and the absence of a marked day-night rhythm. However, in general it may be stated that the actual effect of the environmental factors upon form has not been analyzed.

The conditions which induce sexual reproduction and lead to auxospore formation in the various species of diatoms are also obscure. Likewise, are the conditions stimulating cyst formation in diatoms, dinoflagellates, and coccolithophorids. We know that these processes occur regularly in some species, whereas in others they seem to be rarer, presumably occurring as a reaction to rather special environmental conditions. Germination of resting spores has never been studied in cultures, except for the rather unusual type observed by Gross (1940) in *Ditylum brightwelli*, although it would be of great interest to obtain information on this process in order to further understanding of the annual cycle of many neritic species.

One of the basic features of behavior in plankton diatoms, their ability to maintain populations in the surface layers even during periods of poor growth conditions, is still one of the dark points. The various species seem to react differently in this case also, as some of them maintain small populations in the euphotic layer throughout the year, while others have brief periods of abundance and then disappear. The field observations call for experimental studies, both to investigate further the interesting theory of Gross and Zeuthen (1948) that flotation is due to the maintenance of a relatively high concentration of monovalent ions in the cell sap and also to explain the specific differences in behavior indicated by the field observations.

The effect of submarine light upon the phototaxis of flagellates has been subjected to interesting physiological studies by Halldal (1958), but the specific reactions of most species have yet to be described on the basis of laboratory studies. The observations at sea have shown that migrations take place, and have indicated different reaction patterns for the various species (Hasle, 1950), but experimentally very little has been done here. These are a few of the classical problems that must be solved by experimental means, and they are involved in most of the attempts at understanding the results produced by field surveys. The studies of organic production in the sea by means of Steemann Nielsen's

C^{14} method (1952, 1958a), which have given such valuable results, have again raised many problems related to the actual behavior of the species which are responsible for the observed production.

These examples may suffice to indicate the variety of unsolved problems that are suitable for experimental studies. In spite of the shortcomings in methods which still adhere to the field ecological surveys of marine phytoplankton, it seems obvious, as far as this branch of marine biology is concerned, that Dr. Redfield's warning against too one-sided an experimental approach does not apply at all. The experimental studies have by no means kept pace with the observations of populations in the sea. On the other hand, the little work which has been done on phytoplankton cultures has demonstrated how essential a background of field observations is for a sound evaluation of experimental results. One need refer only to the temperature experiments, which illustrated so clearly the necessity of checking results obtained in the laboratory with the actual distribution pattern of the species in the sea. On the whole, the experience gained from experimental studies supports the generally adopted view that research on environmental influence should be organized in such a way as to establish a close collaboration between workers with a first-hand knowledge of field surveys and skilled experimentators.

With regard to the special branch discussed here, the time seems ripe for an extension of research in the laboratory. The new techniques developed recently should be employed and developed further to exploit more effectively the wealth of observations accumulated through field ecological studies. In view of the fact that the marine vegetation is responsible for at least as large an annual production of organic matter as that of all the terrestrial plants, there seems to be no reason why such an expansion should be made at the expense of work of the survey type. The present efforts in this field seem to be quite out of proportion to the role which these marine plants play in the organic cycle as a whole.

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III. The Deep Sea

Geochemistry and Physics of Ocean Circulation*

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ONE of the problems faced in preparing this paper was that of interpreting the scope of the topic. The broadest interpretation would require a complete coverage of all approaches to the problem of circulation in the deep sea, ranging from the classical density methods to the exciting recent development of deep floats. It was decided to restrict the paper to the use of radioactive isotopes as indicators of oceanic mixing rates.

The main features of the tracer method are well illustrated by the following analogy. Let us assume that a red dye can be obtained which has the unique property of losing its color intensity at an exponential rate when mixed with water. If such a dye were added at a constant rate to one point on the surface of a pool of water, after a steady state had been achieved, one would observe a distribution of color which would depend on the rate of mixing within the pool. If the pool were mixed far more rapidly than the dye decayed, the color would be nearly uniform. If, on the other hand, the mixing rate were far slower than the decay rate, the color would be far more intense at the point of addition than in the extremities of the pool. Computation of the precise time relationships in such a system is complicated, however, by the fact that the color of a given sample of water would be from many little packets of dye each of which had spent different amounts of time in the system. For this reason time estimates computed from color contrast with the source using the simple exponential decay relationship would be ambiguous.

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If a more complex case were used in which the rate of mixing within the pool is altered with time, steady state would not be achieved and the color pattern would change with time. Interpretation of mixing rates from a single color photograph of the system with no knowledge of the manner in which these rates were varying could obviously lead to false conclusions.

The analogy points out that an understanding of mixing patterns in the ocean is a prerequisite of successful application of radioisotopes to oceanic mixing. Thus isotope data are useful only when combined with the proper oceanographic information. The analogy also indicates that a single survey of the concentration of a radioactive isotope in the oceans cannot be correctly interpreted without a knowledge of whether or not deep circulation is essentially a steady state process.

Table I lists the most promising radioisotopes along with their half lives and sources. Of these C^{14} is probably the most useful because of the rather simple geochemistry of carbon in the oceans and because the dissolved bicarbonate in the oceans is communicating with the CO_2 in the atmosphere. The importance of the latter will become clear as the discussion proceeds. H^3, Sr^{90}, and Cs^{137} are difficult to use because of their extremely low concentrations, making measurements tedious and expensive, and because of the complex mode of injection into the system. Recently discovered in oceanic sponges by workers at Scripps, Si^{32} promises to be extremely useful in ocean mixing problems. Koczy has shown that Ra^{226} is being released into the ocean from the sediments. Much of the potential value of the Ra^{226} method lies in

TABLE I. Radioisotopes Applicable to Oceanic Mixing Problem

Isotope	Half Life	Source
C^{14}	5560	Cosmic rays + bombs
Ra^{226}	1600	Ionium decay in sediments
Si^{32}	~710	Cosmic rays
H^3	12	Cosmic rays + bombs
Sr^{90}	28	Bombs
Cs^{137}	30	Bombs

the fact that it is added to the bottom rather than the top of the ocean as is the case for other tracers.

Since, to date, only C^{14} data are available in sufficient quantity to allow any firm conclusions to be drawn concerning mixing rates, I shall demonstrate the potentialities and limitations of isotope tracers through the consideration of radiocarbon alone. The application of C^{14} to oceanographic mixing problems was originally proposed by Ewing and Kulp at Lamont. It has since been successfully used by workers at the Scripps, the New Zealand, and the Stockholm radiocarbon laboratories as well as at Lamont.

The results I shall give are largely unpublished. They have been accumulated over the past four years at Lamont. A large portion of the Lamont staff has contributed to the shipboard and laboratory phases of this work. Drs. Ewing, Gerard, Heezen, and Takahashi have directed the difficult and hazardous operation of collecting 400-liter samples of water and Drs. Kulp, Tucek, and Olson have cooperated at various times in developing various phases of the laboratory procedure.

The procedure used is illustrated in Fig. 1. The sample is collected in a steel barrel which is continuously flushed as it is lowered into the sea. It can be sealed off at the desired depth by dropping a messenger weight from the surface. The water is processed on the deck of the ship by acidification and bubbling with CO_2-free air or N_2. The CO_2 released is absorbed in KOH. The yield is checked on the ship by acidifying a small portion of the KOH and measuring the pressure of the CO_2 released with an oil manometer. Upon return to the laboratory, the CO_2 is released from the KOH by acidification, and purified by absorption on CaO. The radioactivity of the purified CO_2 gas is assayed in a large volume proportional counter with massive iron shielding and anticoincidence shielding. The CO_2 gas is also analyzed in a mass spectrometer in order to determine the concentration of the stable trace isotope C^{13}.

As shown in Table II, the results are first expressed as per mil difference of the radioactivity and hence C^{14} concentration in a sample from that in a standard. In order to eliminate differences resulting from isotope fractionation, all results are normalized to

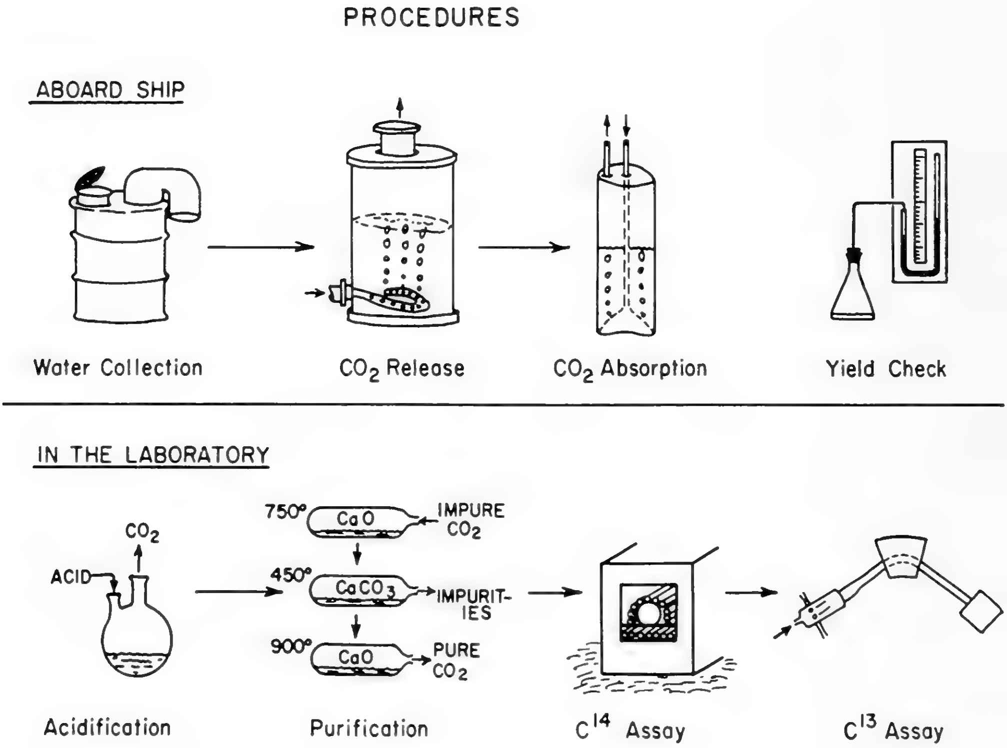

Fig. 1.

a common stable C^{13} concentration. The resulting ΔC^{14} values are then those we would have observed if isotope fractionation did not occur in nature or in the laboratory. In this case if the entire ocean-atmosphere system were being mixed with infinite speed, ΔC^{14} values for all parts of the system would be the same. Since mixing is not sufficiently rapid, the atmosphere which is the birthplace of new C^{14} atoms looks redder than the surface ocean which, in turn, looks redder than the deep ocean. In terms of the above scale the less red the sample the more negative its ΔC^{14} value. The pre-1890 age corrected ΔC^{14} value for the atmosphere has been chosen as the zero on the scale.

Let us first consider the pattern of the results. Figure 2 shows the coverage of surface samples analyzed at Lamont. In addition, results for the Atlantic for latitudes greater than 60° N have been published by Fonselius and Ostlund of the Stockholm group and results for the western South Pacific by Rafter and Fergusson. For simplicity of presentation averages for various reservoirs are given in Table III along with the number of samples analyzed and the standard deviation of the results from the average for each group. For each group the results agree nearly within the error, and no significant variation with current or with geographic location is apparent.

Since many of the samples were collected subsequent to large-scale production of C^{14} during nuclear testing, a small correction for contamination from this source is necessary. This correction has been estimated both by considering only pre-1956 samples (column 2) and by applying a correction based on estimated mixing rates within the system. Fortunately the corrections are small, the largest being ten per mil for the South Pacific. No significant change in the pattern of results is introduced. The resulting corrected averages are summarized in Table IV in the column for 1955.

A further correction for the dilution of the surface ocean C^{14} by industrial CO_2 is necessary. Fergusson has shown through C^{14} measurements on tree rings that the average dilution of the world's atmospheric C^{14} was close to 2% in 1955. Ocean mixing model calculations suggest a dilution of about two-thirds the atmospheric

TABLE II. Conversion of C^{14} and C^{13} Data to per Mil Scale

$$\delta C^{14} = \frac{A_{\text{sample}} - A^{*}_{1890\text{ wood}}}{A^{*}_{1890\text{ wood}}} 1000$$

$$\delta C^{13} = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} 1000$$

$$\begin{array}{ccccccc} \Delta C^{14} & = & \delta C^{14} & - & 2\delta C^{13}\left(1 + \dfrac{\delta C^{14}}{1000}\right) & - & 50.0 \\ & & \text{measured} & & \text{isotope fractionation} & & \text{constant chosen} \\ & & \text{difference} & & \text{correction} & & \text{to make } \Delta C^{14}_{1890\text{ wood}} = 0 \end{array}$$

(Analysis precision averages ±8 per mil)

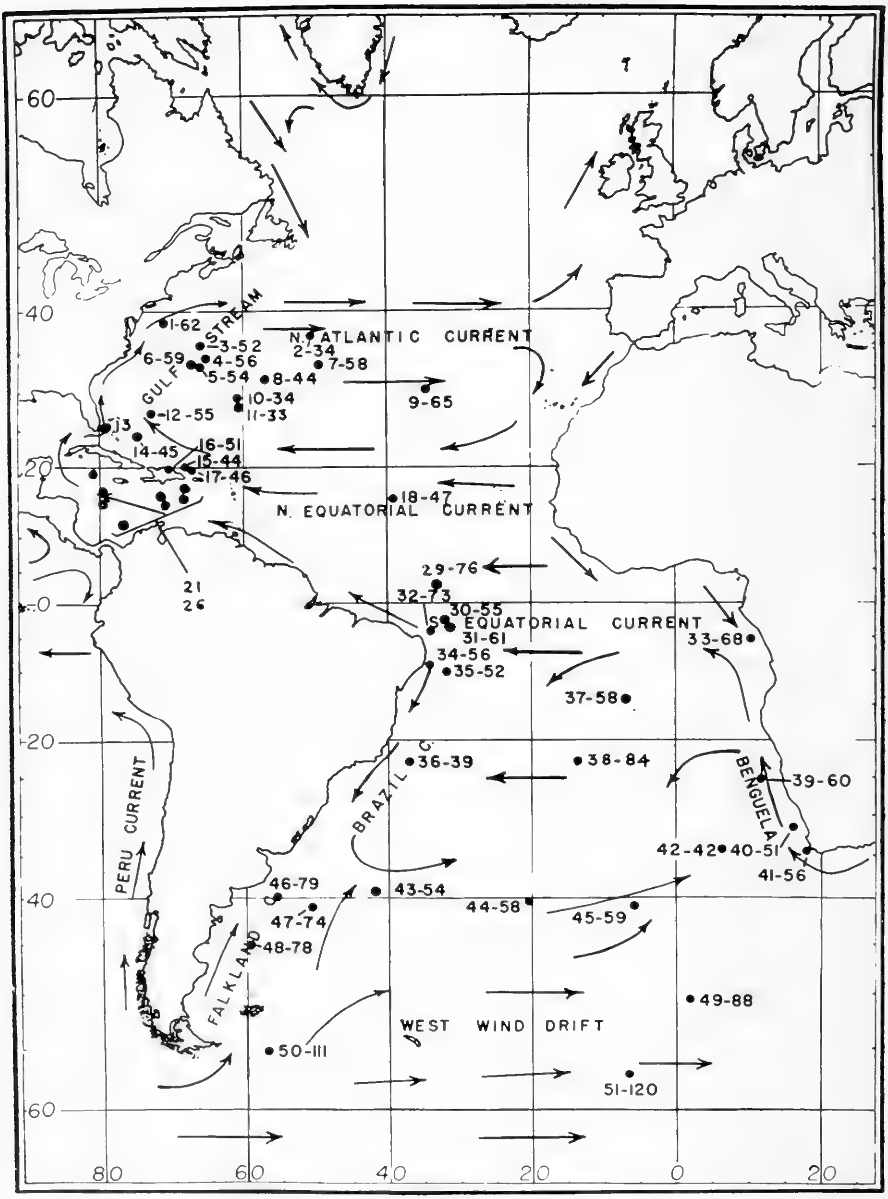

Fig. 2. Location of surface water samples. The first number beside each dot is the index number and the second is the ΔC^{14} value. The arrows show the pattern of surface water movement.

TABLE III. C^{14} Results on Surface Ocean Water

Location	ΔC^{14} Uncorrected for Bomb C^{14}	ΔC^{14} Pre-1956	ΔC^{14} Corrected for Bomb C^{14}
North Atlantic 60–80° N[a]	−35 (3) $\sigma = 2$	—	−40 (3) $\sigma = 2$
North Atlantic 15–40° N[b]	−49 (18) $\sigma = 10$	−47 (10) $\sigma = 9$	−54 (18) $\sigma = 11$
Caribbean[b]	−56 (8) $\sigma = 9$	−56 (8) $\sigma = 9$	−57 (8) $\sigma = 9$
South Atlantic 0–40° S[b]	−57 (16) $\sigma = 10$	—	−63 (16) $\sigma = 9$
Falkland Current[b]	−77 (3) $\sigma = 3$	—	−80 (3) $\sigma = 3$
Antarctic (<3°C)[b, c]	−120 (3) $\sigma = 10$	—	−124 (3) $\sigma = 10$
South Pacific 15–42° S[c]	−41 (16) $\sigma = 9$	−54 (2) $\sigma = 2$	−51 (16) $\sigma = 6$

Note. Quantities in parentheses indicate number of samples.

[a] Fonselius and Ostlund, *Tellus, 11,* 77, 82 (1959).

[b] Broecker *et al., J. Geophys. Research, 65,* 2903–2931 (1960).

[c] Rafter and Fergusson, *Second UN International Conference on the Peaceful Uses of Atomic Energy,* Vol. 18, pp. 526–532 (1958).

dilution for the mixed layer and a somewhat smaller figure for the vertically mixed reservoirs at the extremes of the ocean. Again the correction is sufficiently small that it does not have a large effect on any conclusions drawn. Thus the corrected values in the 1890 column may be taken to represent concentrations of C^{14} in the surface ocean prior to man's tampering with the system.

The results suggest a difference of ~ 12 per mil between the average North and South Atlantic mixed layers. The Caribbean has a value intermediate between the two, as would be expected, since it receives water from both the North and South Atlantic mixed layers. A sharp drop in C^{14} occurs on crossing the Antarctic convergence. Rafter and Fergusson observe a quite similar sharp drop in the South Pacific. Fonselius and Ostlund find, in contrast, slightly higher values in the cold water of the northern-most Atlantic. The South Pacific average is quite close to that for the Atlantic.

TABLE IV. Industrial CO_2 Effect Correction

Location	ΔC^{14} 1955	ΔC^{14} 1890
North Atlantic (60–80° N) (3)	−40	−34
North Atlantic (15–40° N) (18)	−51	−37
Caribbean (8)	−57	−43
South Atlantic (0–42° S) (16)	−63	−49
Antarctic (<3° C) (3)	−124	−121
South Pacific (15–42° S) (16)	−51	−37
Atmosphere	−21	0
Average ocean	−58	−46

Note. Quantities in parentheses indicate number of samples.

For the deep water, the sample locations in the Western Basin and Eastern Basin of the Atlantic are shown on the vertical profile in Fig. 3. The depth and latitude coverage are fairly complete between 40° N and 40° S. The areal distribution of the sampling is shown in Fig. 4. All main water masses have been sampled.

Again since consideration of individual results is impractical in the time available, averages are shown in Fig. 5. One broad feature is that water originating at the Antarctic surface in all cases has a lower ΔC^{14} value than that originating in the northern North Atlantic. This pattern is consistent with that observed in the surface waters, the concentration being lower in the Antarctic than in the northern-most Atlantic. Except for a layer of high C^{14} water between 1200 and 2500 m in the Western Basin, the deep waters of the North Atlantic and those which penetrate the South Atlantic from the North are nearly uniform in C^{14} concentration, 100 per mil of 10% below the atmospheric value. Bottom samples do not differ significantly from those taken in the core of the mass, and there is no significant change with latitude. As shown in Table V, there appears to be a lower C^{14} concentration in the deepest water of the Eastern Basin than in the Western Basin suggesting a longer residence time in the Eastern than in the Western Deeps. Above the ridge the two basins apparently mix quite rapidly.

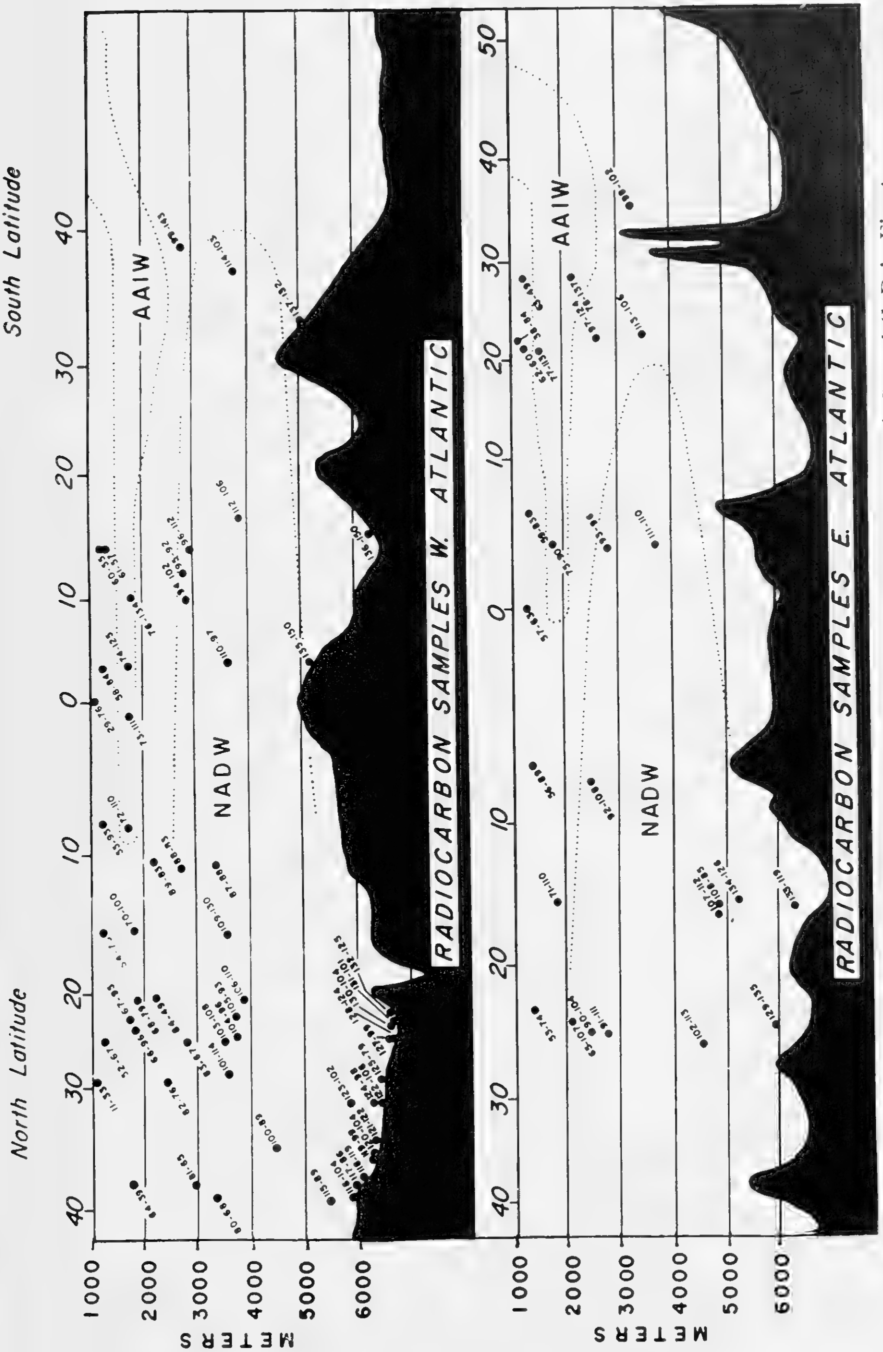

Fig. 3. Subsurface sample locations projected onto depth profiles along A–B and C–D in Fig. 4.

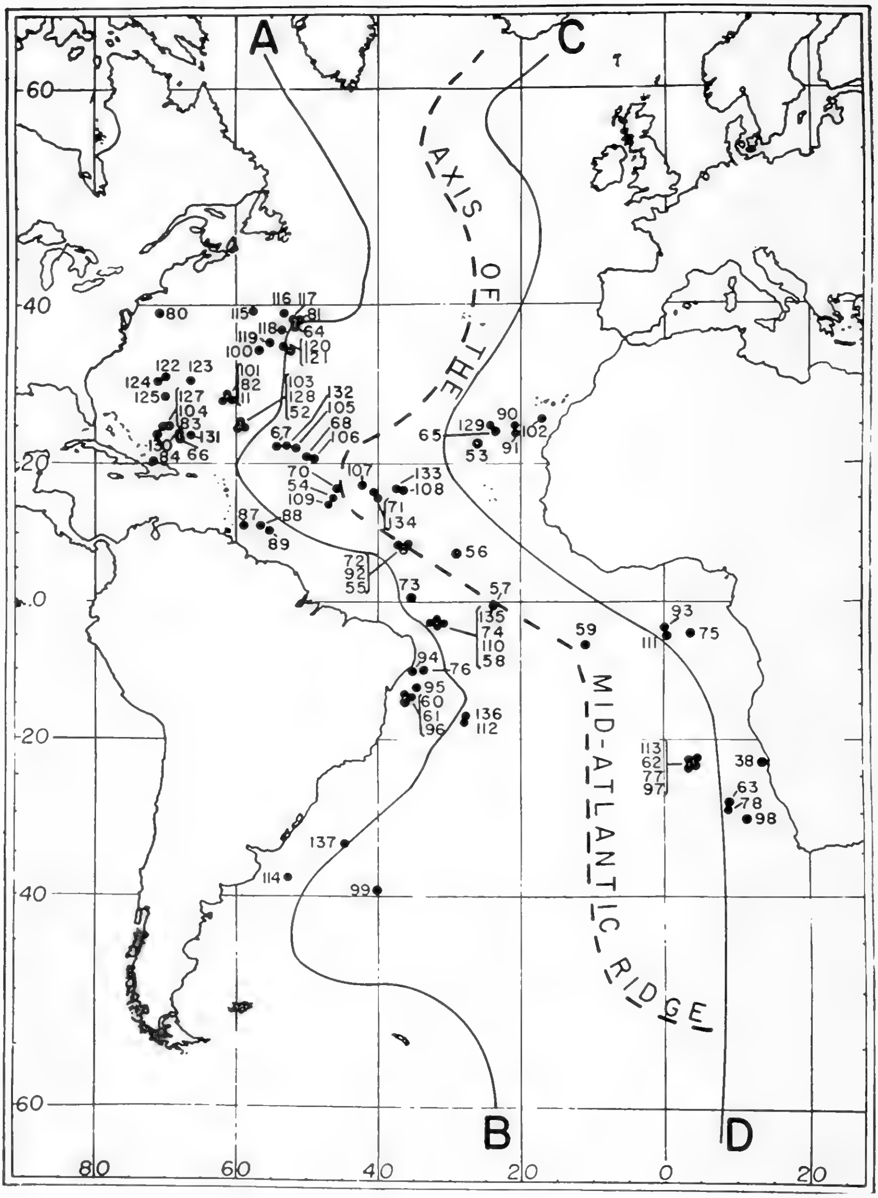

Fig. 4. Location of subsurface samples.

TABLE V. North Atlantic Deep Water Western versus Eastern Basin

Depth, meters	Western Basin	Eastern Basin
2500–4000	−103 (7)	−107 (7)
>4000	−100 (15)	−127 (3)

Note. Quantities in parentheses indicate number of samples.

The evidence for a C^{14} maximum layer between 1200 and 2500 m is summarized in Fig. 6. Samples taken in the Western Basin of the North Atlantic have 20 to 40 per mil more C^{14} than those above and below as well as those to the south and east at the same depth. Samples from the southern South Atlantic at this level show even lower values. From their lower salinities it is probable that these samples are of Antarctic rather than North Atlantic origin.

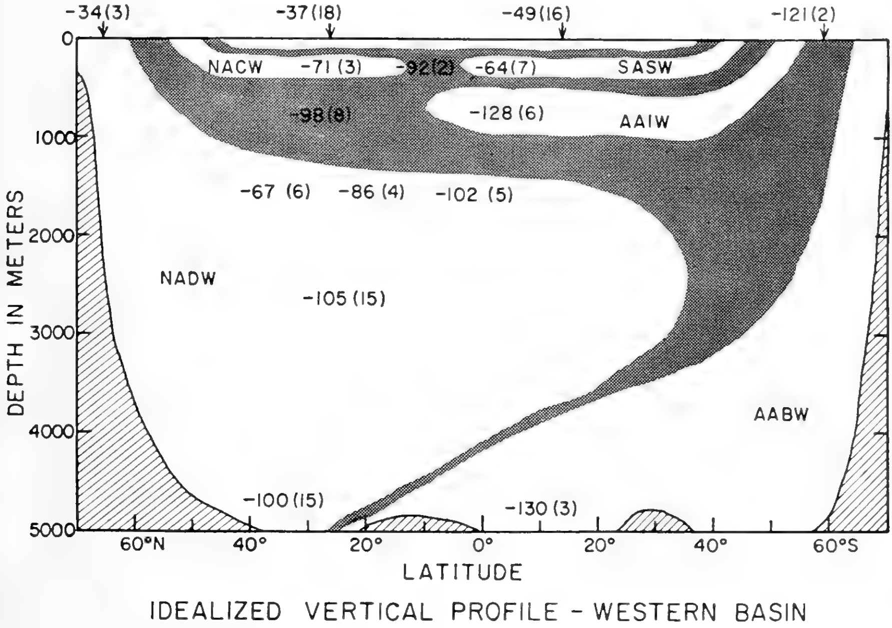

Fig. 5. ΔC^{14} averages for various water masses. Numbers in parentheses indicate number of samples.

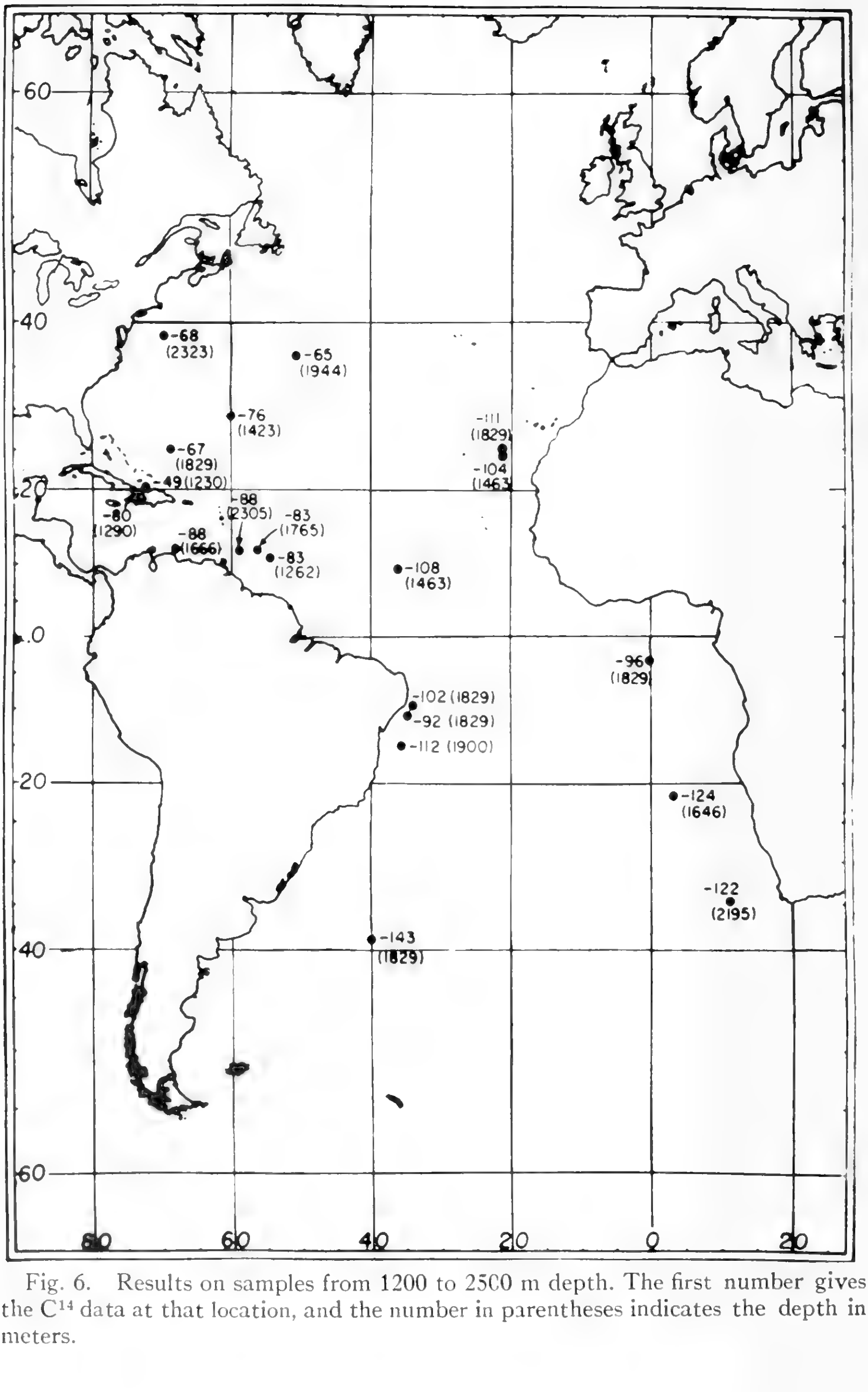

Fig. 6. Results on samples from 1200 to 2500 m depth. The first number gives the C^{14} data at that location, and the number in parentheses indicates the depth in meters.

Figure 7 shows the C^{14} data for the central waters plotted on a T-S diagram. Note for the South Atlantic central waters (SACW) that the ΔC^{14} values are lower for lower temperatures. This is consistent with the pattern observed in the surface waters at the southern end of the ocean, therefore lower C^{14} for lower temperature.

Crude ages can be assigned to the deep waters of the Atlantic in the following way. If it is assumed that the deep water at the time of descent had a C^{14} concentration the same as that observed today in the source region for the mass, the mean residence time of water in the mass can be estimated from the difference between the value at the surface and that characterizing the mass at depth. Such residence times for deep waters originating in the North Atlantic are given in Table VI. At best the estimates may be good to ±100 years, and at worst they probably represent maximum estimates of the residence time. With the exception of the central water and the C^{14} maximum layer, the times are close to 500 years.

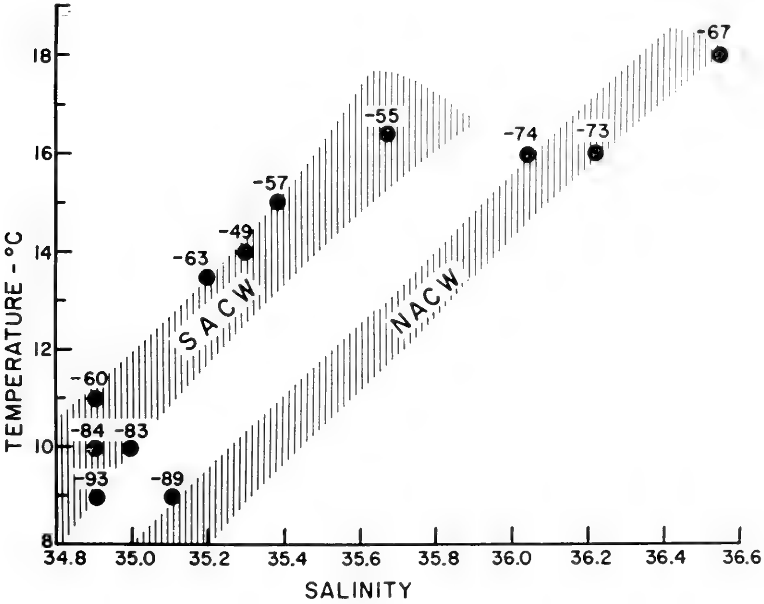

Fig. 7. ΔC^{14} results for samples from the central water systems as a function of temperature and salinity.

Table VI. Deep Water of North Atlantic Origin

Depth, meters	ΔC^{14}, ‰	Difference from Source, ‰	Crude Age, years
Surface (19)	−35		
200–400 (3)	−71	36	300
800–1100 (8)	−98	63	600
122–2500 (7)	−102	67	650
1200–2500 (10) (Western Boundary)	−75	40	350
2500–4000 (15)	−105	70	700
>4000 (15)	−100	65	650

Note. Quantities in parentheses indicate number of samples.

Similar estimates for the South Atlantic are given in Table VII. The mean residence time for the Antarctic bottom water (AABW) is less than 200 years. Since few measurements exist for surface waters in the South Atlantic and Antarctic with temperatures from 4 to 8 degrees or less than 1 degree, a greater uncertainty must be attached to the Antarctic bottom water and Antarctic intermediate water (AAIW) residence times. The data suggest shorter residence times than for waters of North Atlantic origin.

In order to evaluate whether the system is in steady state as assumed for these age calculations, a model of the entire ocean-atmosphere system must be constructed. Since both sufficient C^{14} data and details of oceanic mixing patterns are lacking, a truly

Table VII. Deep Water of South Atlantic Origin

	ΔC^{14}, ‰	Difference from Source, ‰	Crude Age, years
Surface 1–3° (3)	−121		
Surface 3–7° (2)	−90		
Surface 12° (16)	−49		
200–400 m (6)	−64	15	120
600–1200 m (6)	−128	38	300
1200–2500 m (3)	−130	9	75
>500 m (3)	−144	< 23	< 200

adequate model is not possible. A grossly simplified model preserving only the main features of the system is still useful, however. The ocean-atmosphere system has been broken up into eight reservoirs which are considered to be internally well mixed. The reservoirs chosen are defined in Table VIII. The cold region north of 55° N in the Atlantic and north of the Bering Straits is defined as the Arctic and that south of 55° S as the Antarctic reservoir. The mixed layer of the oceans assumed to extend to 100 m depth is broken into three parts, North Atlantic, South Atlantic, and Pacific + Indian Oceans. Existing radiocarbon data allow no detailed division of the large Pacific and Indian Ocean systems. The area presented by each reservoir to the atmosphere and the total carbon stored in each reservoir are shown in the last two columns. A diagram of the model is given in Fig. 8. The mixing between reservoirs is assumed to be as shown by the arrows. The Atlantic is characterized by a northward transfer at the surface and southward transfer at depth. The Pacific + Indian Ocean surface and deep reservoirs communicate only at the south end of the ocean. The Atlantic and Pacific communicate through the Antarctic. No mixing is assumed across the main thermocline in either ocean. The exchange of CO_2 between the ocean and atmosphere is assumed to be independent of geographical location.

Measured values are used to estimate the average ΔC^{14} value

TABLE VIII. Oceanic Mixing Model

Reservoir[a]	Latitude Range	Depth Range, meters	Surface Area, square meters	Volume, moles C
"Arctic"	>55° N	Entire	15×10^{12}	40×10^{15}
North Atlantic surface water	55° N–5° N	<100	40×10^{12}	9×10^{15}
South Atlantic surface water	5° N–50° S	<100	40×10^{12}	9×10^{15}
North Atlantic deep water	55° N–50° S	>100	—	655×10^{15}
Antarctic	>50° S	Entire	45×10^{12}	420×10^{15}
Pacific + Indian Ocean surface water	<55° S	<100	220×10^{12}	50×10^{15}
Pacific + Indian Ocean deep water	<55° S	>100	—	1980×10^{15}
Atmosphere	Entire	Entire	360×10^{12}	57×10^{15}

[a] Assume uniform ΔC^{14} in each reservoir.

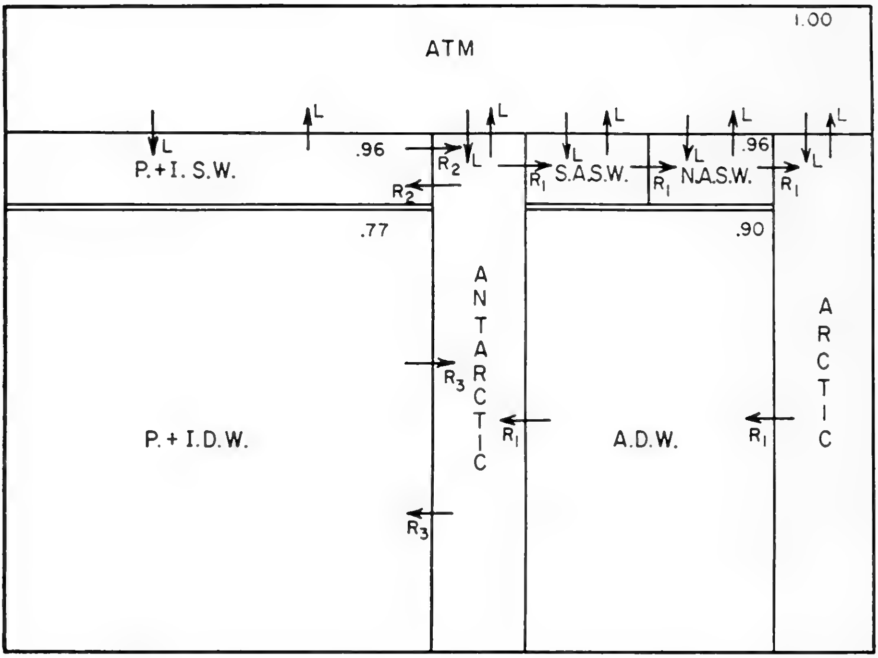

Fig. 8. Box model of large-scale oceanic mixing. Arrows indicate allowed modes of transfer between reservoirs. Numbers refer to relative C^{14}/C^{12} ratios.

for four of the reservoirs. The value for the deep Pacific is 0.77 of the atmospheric value or -230 on the per mil scale, for the deep Atlantic, 0.90 or -100 on the per mil scale, for both the surface Pacific and the surface North Atlantic 0.96 or -40 on the per mil scale. This uniquely determines the four unknown rates, R_1, R_2, R_3, and L, and the three undetermined concentrations, the C^{14} concentrations in the Arctic, Antarctic, and South Atlantic surface water (SASW), are fixed mathematically. These results are shown in Table IX. The concentrations fixed by the model for the Antarctic, Arctic, and South Atlantic surface water agree satisfactorily with available measurements. The CO_2 exchange rate between atmosphere and ocean agrees well with that of Craig based on a simpler but somewhat similar model. The rate of net northward transport in the Atlantic is consistent with the empirical estimate of 430 × 10^{12} moles C/year computed from Sverdrup *et al.*, *The Oceans*.

TABLE IX. Results of Model Calculations

	Model	Empirical Estimate
ΔC^{14} Antarctic	$-107‰$	$-121‰$
ΔC^{14} Arctic	$-32‰$	$-34‰$
ΔC^{14} SASW	$-60‰$	$-49‰$
CO_2 Transfer rate	20 moles/m^2 yr	—
R_{Atlantic}	930×10^{12} moles C/yr	430 moles C/yr
$R_{\text{PSW--Antarctic}}$	1850×10^{12} moles C/yr	
$R_{\text{PDW--Antarctic}}$	1525×10^{12} moles C/yr	

Mean residence times of water molecules in each oceanic reservoir with respect to transfer to another reservoir are given in Table X. Regardless of the simplicity of the model and lack of coverage in the Pacific and Indian Oceans it is clear the deep oceans are being renewed with a time scale of the order of magnitude of 1000 years.

TABLE X. Mean Residence Times Based on Model

Location	Time, years
Arctic	45
NASW	10
SASW	10
NADW	600
Antarctic	100
P + ISW	25
P + IDW	1300

Three independent checks on this model suggest themselves. The first, as summarized in Table XI, is a comparison with tritium

TABLE XI. Tritium Crosscheck

Assumptions
1. Tritium addition rate approximately uniform over surface of ocean
2. Pre-bomb tritium concentration in NASW 1 tritium unit.

Required production rate
2 tritium atoms/cm^{2}sec

Independent estimates
$\sim$ 1 tritium atom/cm^{2}sec

data. The only reliable estimates of the pre-bomb concentration of tritium in the oceans are those for the North Atlantic surface water based on measurements by Begemann at the University of Chicago and by Giletti at the Lamont Geological Observatory, both investigators finding a pre-bomb level of 1 tritium per 10^{18} hydrogen atoms. With the above model and the mixing rates obtained from C^{14} data, the tritium concentrations of each of the other ocean reservoirs as well as the required input rate are uniquely determined. It is interesting to compare the production rate of tritium computed in this manner with those made by entirely independent means by other investigators. The value of two T atoms/cm^2 sec is satisfactory agreement with independent estimates of one T atom/cm^2 sec.

A second internal check is to determine whether the industrial CO_2 added to the atmosphere over the past 100 years will be transferred into the ocean at a sufficient rate to satisfy the C^{14} data on tree rings obtained by Suess, Fergusson, and others. The results are shown in Fig. 9. The curve based on the model must

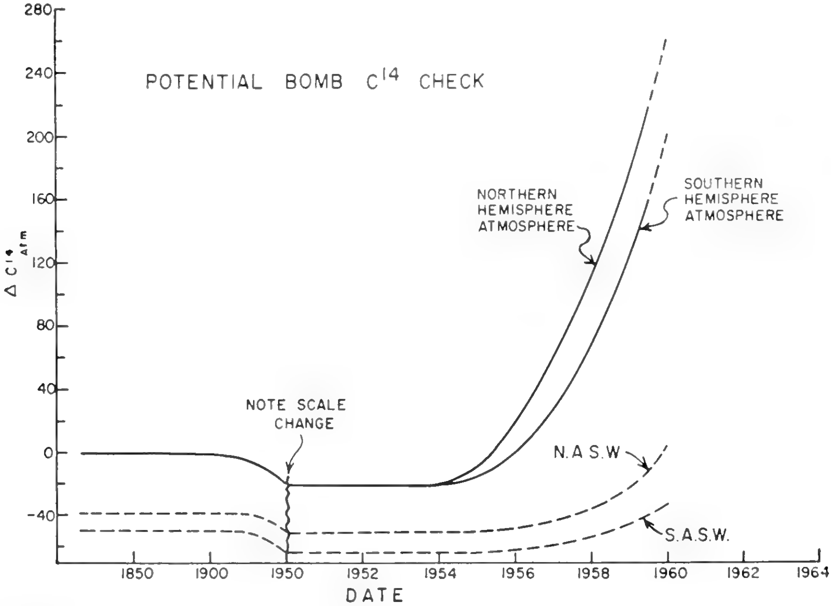

Fig. 9. Comparison of observed and predicted industrial CO_2 effect on atmospheric C^{14}/C^{12} ratio.

be considered an upper limit since no account of storage of humic materials in soils has been made. If these humic materials are renewed each 30 years and if existing estimates of their abundance are reliable, the two curves would agree.

A potential further crosscheck method involves C^{14} produced by bombs. Figure 10 shows how the atmospheric C^{14} concentration has changed since 1850. Following a small drop resulting from the addition of industrial CO_2 to the system a rapid rise commenced in 1955. Currently the southern hemisphere lags behind the northern because the majority of the testing has taken place north of the equator. This bomb C^{14} is gradually being transferred to the ocean. Estimates based on the model suggest that the surface water should now be running about 30 per mil higher than in the pre-bomb era. Estimates based on bomb production to date suggest that the surface ocean will rise about 100 per mil during the next 10 years. This rise will provide an extremely valuable tracer for near surface ocean circulation. Rather than greatly confusing attempts to apply isotopes to oceanic mixing problems,

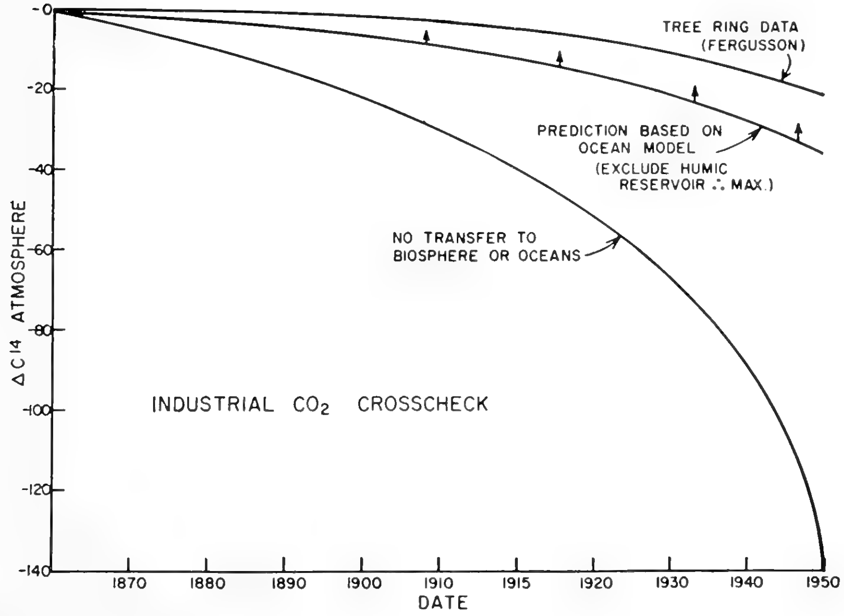

Fig. 10. Variation in C^{14}/C^{12} ratio in atmospheric CO_2 over the last 100 years.

as was the case with tritium, bomb production greatly enhances the use of C^{14} without introducing any important disadvantages.

Having shown that the model selected provides a reasonable approximation to the true large-scale mixing within the ocean-atmosphere system, the model can be used to estimate the effects of changes in circulation rates. Assuming that the rate of transfer of CO_2 between the ocean and atmosphere has remained constant with time and that the total amount of C^{14} has remained the same, Table XII gives the changes in the C^{14} concentration in the various reservoirs for the case where oceanic mixing rates are doubled and for the case where they are halved. The most interesting feature of the results is the large change in the C^{14} concentration of atmospheric CO_2 which would be produced by such changes. The atmosphere would fall 70 per mil in concentration if ocean circulation rates were doubled and rise 120 per mil if halved. Measurements by numerous radiocarbon laboratories of the C^{14} concentration in tree rings back to 2000 years in age suggest changes of up to but probably not greater than 2 per cent either side of the 1890 value. On the assumption that these changes are the result of variations in ocean circulation rates rather than to changes in the production rate of C^{14} they correspond, as shown in Fig. 11, to limits of ±20% on circulation rate changes. A 15% decrease in circulation rate would, after steady state was reestablished, result in a 20 per mil rise in the C^{14} concentration in atmospheric CO_2 and a 20% increase in rate to a 20 per mil drop. The method is, of course, sensitive only to worldwide changes of a period at least

TABLE XII. Effect of Changes in Rates of Ocean Circulation on Distribution of Radiocarbon between Oceans and Atmosphere

	ΔC^{14} Present Distribution	ΔC^{14} If Rates Double	ΔC^{14} If Rates Halve
Atmosphere	0	−71	+121
Average surface ocean water	−46	−121	+79
NADW	−104	−138	−64
P + IDW	−230	−208	−265

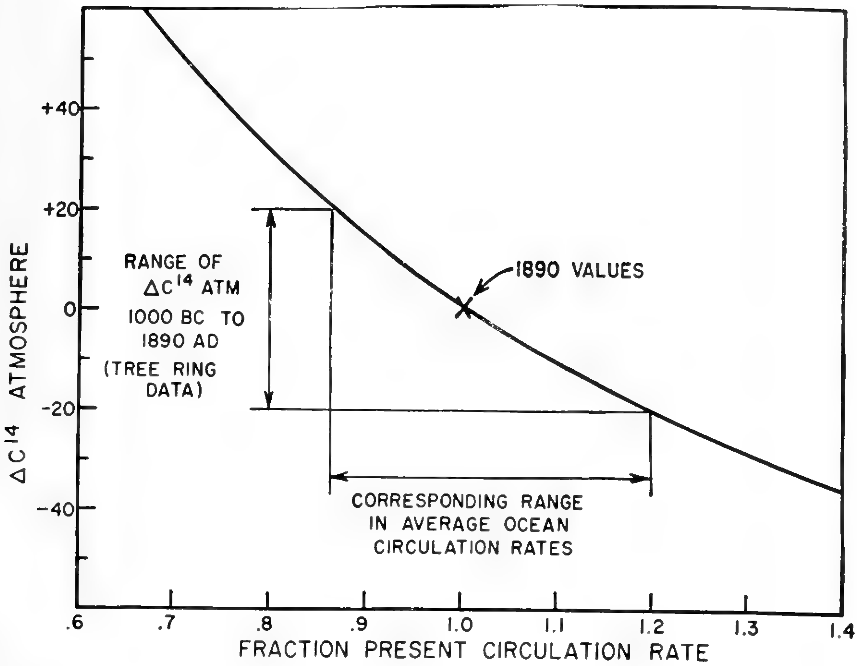

Fig. 11. Dependence of atmospheric C^{14}/C^{12} ratio on oceanic mixing rate.

several decades. Short-term worldwide fluctuations and random local changes would not show up in tree ring data.

In summary, the following conclusions are drawn concerning the use of radioactive tracers in studying large scale ocean circulation problems.

1. As in most investigations, one of the main needs is more data and a more complete correlation of the data with available oceanographic information. This will allow more adequate circulation models to be set up.

2. C^{14} appears to be the most powerful of these tracers. Its unique advantages are, first, that tree ring data allow the steady state assumptions to be tested and evaluated, and second, that bomb-produced C^{14} will provide an independent check on many steady state predictions. Other long-lived isotopes, such as Ra^{226} and Si^{32}, also should prove extremely valuable in their own right

and even more valuable when used in conjunction with C^{14} and with each other.

3. Isotope methods are best for large-scale problems. Mixing within given masses of water is in many cases apparently too rapid to give rise to appreciable concentration differences. In this respect the method nicely supplements the deep float method which yields considerably more detailed information in local areas.

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Certain Quantitative Characteristics of the Pelagic and Bottom Life of the Ocean*

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AT present it is impossible to give a sufficiently complete picture of the composition, the vertical and horizontal distribution, the ecology and the history of the pelagic fauna throughout geologic time. This is especially difficult for the abyssal fauna. Therefore, I have taken the liberty of enlarging the scope of my report and have attempted to make generalizations about a number of problems.

Our knowledge of the systematics of the abyssal fauna is far from complete. According to Vinogradova's (1959) accurate estimate for Spongia, Coelenterata, Cirripedia, Isopoda, Decapoda, Pantopoda, Asteroidea, Echinoidea, Crinoidea, Holothurioidea and Pogonophora, 189 species have been found in depths greater than 4000 m. Bruun (1956, 1957) listed 127 species (exclusive of Foraminifera and Pogonophora) in depths exceeding 6000 m. This figure should now be doubled with the addition of the Foraminifera (78 species), Pogonophora (17 species), Echiuroidea (5 species), and other Crustacea and Echinodermata. The qualitative impoverishment noticed in various groups varies with depth. The change in the number of species with depth is also evident for the following groups: Polychaeta, Pericarida, Pogonophora, Asteroidea and Holothurioidea. Furthermore, it is of interest to note that in going from midlatitudes (north and south of 40°) to the equatorial region (between 40°N and 40°S), the total number of species (Table I)

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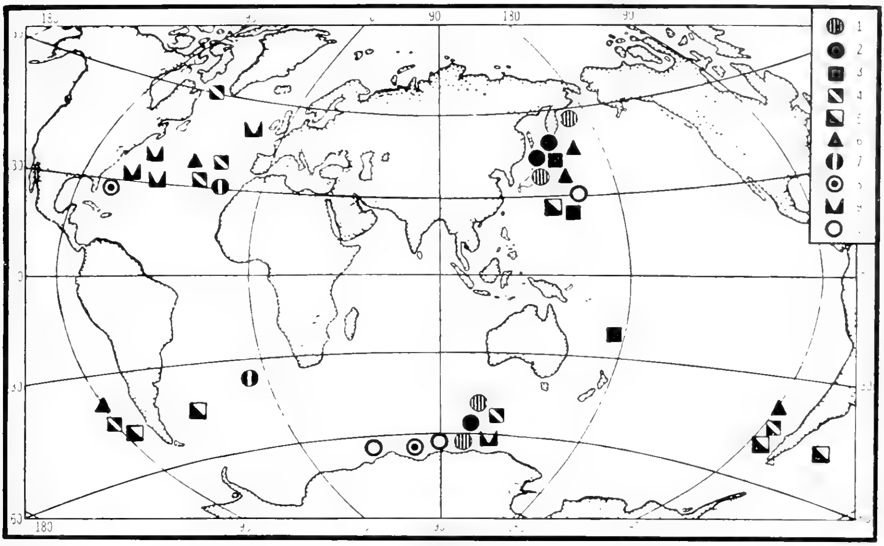
TABLE I. Approximate Number of Benthic Animal Species at Various Latitudes and in Various Depths
(180,000 accepted as total number of marine species)

Dwelling Realm	In All	North of 40°N		From 40°N to 40°S		South of 40°S	
		No.	%	No.	%	No.	%
Shelf zone	180,000	15,000	8.3	150,000	83.3	?	8.3?
Below 2000 m (Vinogradova, 1959)	1,080	439	40.7	591	54.7	274	25.4
Below 4000 m (Vinogradova, 1959)	189	61	32	98	52	33	16

belonging to the fauna of the continental shelf increases approximately ten times. In contrast, the number of species at depths exceeding 2000 m in both zones is approximately the same. This suggests that the migration of animals to the great depths in high and midlatitudes is less complicated than in the tropics.

Recently the biogeographical homogeneity of the abyss has become quite obvious and the great depths have been called the "realm of monotony." However, now it is possible to propose a different viewpoint. Vinogradova (1959), who has studied this problem over a period of years, subdivides the abyss into three realms, six subrealms, and eight zoogeographical provinces. These subdivisions may be even further subdivided in the very near future. This likelihood is particularly pronounced in the distinct bipolar distribution of the abyssal fauna (Fig. 1). It is also noteworthy that a circumtropical distribution of the abyssal fauna is equally pronounced. Indeed, there are some relic forms in the abyssal fauna of these areas. Two species of *Neopilina* as well as both species of *Spinula* (Dall, 1908) are limited to depths of about 3000 m off the west coast of Central America.

What limits representatives of the abyssal fauna (with but few exceptions) to areas with similar environmental conditions, such as temperature, salinity, and the oxygen content of the water? Possibly, to some extent, this may be ascribed to the bottom topography and to pressure, but it is unlikely that these are the only factors concerned. Perhaps the chemistry of the bottom



1. *Phascolion lutense* (Sipunculoidea), 3606–7340 m
2. *Tatjanellia grandis* (Echiuroidea), 2970–3400 m
3. *Scina wagleri* var. *abyssalis* (Amphipoda), >6000 m
4. *Munidopsis antonii* (Decapoda), 2520–3900 m
5. *Glyphocrangon rimapes* (Decapoda), 2510–3120 m
6. *Nymphon procerum* (Pantopoda), 2430–4600 m
7. *Hymenaster anomalus* (Asteroidea), 2059–2608 m
8. *Kolga nana* (Holothurioidea), 2245–4750 m
9. *Culeolus shumi* (Ascidia), 2894–4716 m
10. *Culeolus murrai* (Ascidia) 3397–4630 m

Fig. 1. Some examples of bipolar distribution of the abyssal fauna.

sediments or of the bottom water layer just above the bottom may determine their distribution. This is a mere hypothesis. Perhaps also, the tectonic processes due to volcanic activity, the outcropping along lines of fracture, the accumulation of radioactive substances and rare elements in a particular area, a certain gas in the near-bottom layer may all contribute to defining local biogeographical provinces. These might provide effective barriers for abyssal organisms which are especially sensitive to one or another of these factors. I illustrate this point with a photograph from the eastern Pacific taken by my son, N. Zenkevitch, at a depth of 4000 m (Fig. 2). What else can be compared with these "cobblestones" of iron-manganese concretions other than a chemical flask in which crystallization takes place artificially?

Of special interest is the problem as to when the abyssal fauna originated and the old and primitive characteristics of its representatives. Recently, a lively discussion has arisen about this (Bruun, 1956; 1957; Zenkevitch, 1958; Menzies and Imbrie, 1958; Birstein, 1959; Zenkevitch and Birstein, 1960). In this discussion doubt has been cast upon the widely accepted view that the intrinsic characteristics indicating that old and primitive forms belong for the most part to the abyssal fauna rather than to that in shallow water and that in the former there is a greater number of "living fossils." Bruun, on the contrary, believes that the present abyssal fauna is correlated with a geologically young formation. Menzies and Imbrie (1958) state that the "shallow water marine, the fresh water and the terrestrial environments have more archaic kinds of life than the abyssal marine environment." This question is of great significance and requires further discussion. We are inclined to believe that the first viewpoint is the more probable. As for Bruun's reasoning, I must refer the reader to the detailed analysis of the problem made

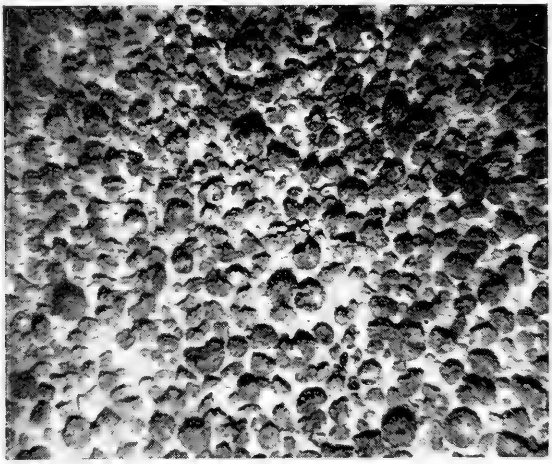


Fig. 2. Iron-manganese concretions at the bottom of the east Pacific, depth 4545 m. (Photograph after N. Zenkevitch.)

by Birstein (1959), as this report seems to me to be quite convincing.

As for the argument made by Menzies and Imbrie, it is first noteworthy that the selection of material by these authors for their analysis is entirely artificial and does not solve the problem, i.e., "these groups were selected because for each there was available bathymetric and paleontologic information that was considered reliable enough to give useful results" (Menzies and Imbrie, 1958). Since the authors state that "for the Echinodermata, Arthropoda and Mollusca we have not been able to assemble quantitative data on both age and depth distribution," it is clear, as the authors themselves pointed out, that the most characteristic groups of the present abyssal fauna do not come within the scope of their analysis (i.e., Echinodermata, Arthropoda and Mollusca). To this enumeration, we have added the Polychaeta, Pogonophora, and Echiuroidea. I doubt that the authors include the most typical representatives of the abyssal fauna related to these groups, which either no longer inhabit the shallow-water zones, never have lived there, or have originated in the ocean depths themselves. If we disregard this last assumption, the endemic species of the ocean depths should be considered as relics of earlier geologic periods, even though they have not been found even as fossils in shallow water. It is necessary to take into account the fact that abyssal deposits are unknown to paleontologists. If fossils of Pogonophora are not yet available, it should be ascribed to the fact that the paleontologists do not yet recognize their tubes or to their great age which dates back to the Proterozoic. In the Paleozoic, they were already inhabitants of the ocean depths.

To date about seventy species (not all of which have yet been described) related to this group have been found in the ocean depths. The Pogonophora doubtlessly are very primitive species. The abyssal Polychaeta and Echiuroidea are likewise primitive. Menzies and Imbrie suppose that *Neopilina* is the only representative of the abyssal fauna discovered thus far as a fossil. But, as you know, there are already two Neopilinas. Six species of the genus *Spinula* (Malletiidae, Bivalvia) have been taken in the abyss of the Pacific. Their known related forms are from Silurian deposits. The family Brisingidae (Asteroidea) is the most primitive form of the order Forcipulata. It is abundantly represented in the ocean depths. Seven of the seventeen genera in this family are represented by forty-one species in abyssal depths.

Phanerozonia, the most primitive order known from the Mid-Cambrian, also has some representatives. The Porcellanasteridae is the most primitive family in this order. Furthermore, forty-seven species of this family live only in the ocean depths. Fifteen species of Echiuroidea, a very old and primitive group of worms, are known to inhabit the abyssal depths only. To these could be added a great number of Crustacea and Polychaeta. There are 151 species, even without the latter, i.e., at least 15% of all species taken from depths exceeding 2000 m. If we consider only forms related to fossils from the Paleozoic, they alone contribute 96 species, i.e., about 8% of all known deep species. In contrast, only twelve old and primitive marine species are cited by Menzies and Imbrie from shallow water (even with the addition of another 4 species of *Nautilus*) and these form only 0.005% of the total in shallow seas, i.e., they are only one-thousandth of the total. Except for the Foraminifera, the groups these authors are chiefly concerned with (Bryozoa, Brachiopoda, Scleractinia) are definitely not characteristic of the abyssal fauna.

Doubtless the abyssal fauna has young representatives (geologically speaking) and lone representatives. Similarly, the shallow-water fauna contains archaic, primitive forms. However, this fact does not preclude our basic position. Thus, the abyssal fauna is distinguished by its obvious slow evolutionary development, which took place in a very homogeneous environment. This is shown by the exceedingly high dispersal rate of its inhabitants. Not only the abyssal fauna, but also the cave-dwelling fauna (to a less extent), the soil-inhabiting fauna and the interstitial fauna of the beaches along the seashore lag behind this evolutionary development. The supposition is that a rapid formation of the abyssal fauna is in conflict with a slow formation in waters lacking such a fauna throughout its geological history. The Japan Sea, for example, has none. The peculiar abyssal fauna in the deep depression of the Polar Basin is still in its infancy. We believe that the characteristic abyssal fauna reflects the particular ocean's history and the faunal development in the surface layers, because it has a slower evolutionary development in comparison with the shallow-water fauna. This explains the presence of old and primitive forms.

Our present knowledge of the taxonomy and distribution of the oceanic flora and fauna, more especially the pelagic fauna, makes it possible to focus attention on their significance in suggesting the permanent character or at least on the great antiquity of the oceanic trenches themselves. However, some preliminary assumptions must be made: (1) the paleontologists thus far know nothing of the pelagic sediments; (2) the taxonomic differentiation of fauna in various parts of the ocean should furnish evidence indicating the age of the local differentiation; (3) the pelagic fauna is characteristically of great antiquity. If these assumptions are true, it is obvious that the difference today between the surface and deep-water faunas in the Atlantic and Pacific oceans, as well as the availability of the pelagic fauna, requires the further assumption that the oceanic depths are permanent. This is incompatible with the idea of a local discontinuity in these depths. If this were the case, the vertical and horizontal isolation of the faunal types would not be shown—the oceanic fauna would inevitably be more homogeneous, and the endemic fauna would not have become individualized in separate parts of the world ocean.

At present, one more picturesque chapter in oceanic history is being unfolded. Our knowledge in this field is insufficient even in shallow-water zones. The statement made at the last meeting of the Special Committee on Oceanic Research (SCOR) in September 1958 was true: "Except in a few cases it is not possible to assess the sizes of marine populations at different trophic levels, or the biological productivity on a worldwide basis. Quantitative data are absent or inadequate in many regions, while in others intercalibration of collecting and assay methods is necessary." One cannot disagree with Thorson's (1958, p. 68) statement that "the first stage . . . must be a thorough quantitative mapping of the level-bottom communities" and that "very little work has so far been done in the United States."

The Soviet oceanographers can hardly be charged with this omission. In thirty-five years of marine investigations, the quantitative method has been used in the study of the biomass, the bacterial productivity, the marine plankton, and the animals and plants of the benthos. Now Soviet investigators have collected planktonic and benthic data for many years from several seas of the USSR, especially in the Barents, Bering, Okhotsk, Azov, and Caspian seas and constructed recent detailed charts for plankton and benthos distribution in all the seas of the USSR. Thanks to the work aboard the *Vitjaz* and *Ob* throughout the past decade, quantitative data on the bacterial, plankton, and benthos distribution in abyssal zones of the Pacific and Indian oceans and in Antarctic waters at great depths and for bottom communities are now available. The density of the benthos along the coast amounts to a few kilograms, but on the ocean bed it drops to 100, then to 50, and finally to 10 mg/m^2 (i.e., it is one-millionth that of the coastal areas) (Fig. 3).

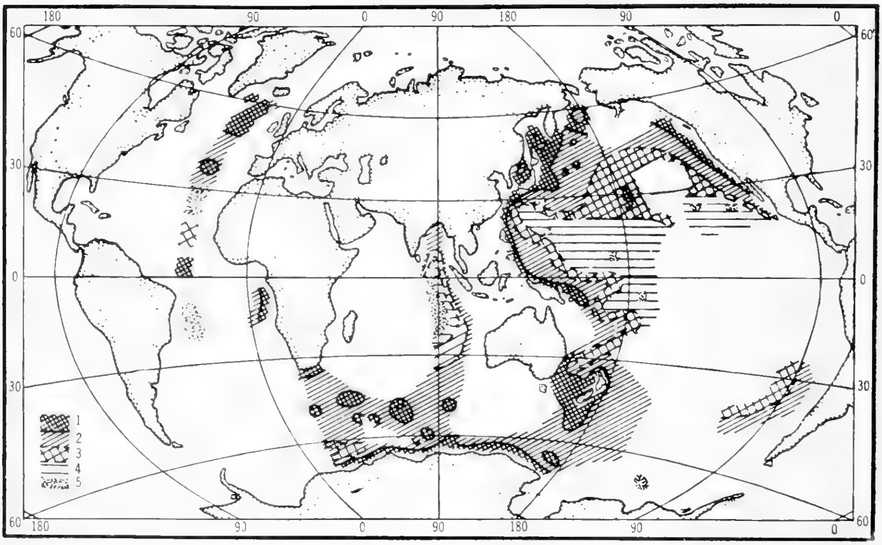


Fig. 3. The quantitative benthos distribution in the northern Pacific and in the eastern part of the Indian Ocean at depths exceeding 2000 m. Benthos biomass measured in grams per square meter: 1, more than 1; 2, 0.1–1; 3, 0.05–0.1; 4, 0.01–0.05; 5, less than 0.01.

In 1959 aboard the *Lomonosov*, a series of samples was obtained with a bottom sampler in the Atlantic along the 30th meridian (from Greenland to 20°S). A preliminary examination of this material (Kusnetzov, 1960) shows that the quantitative distribution of both the pelagic and bottom fauna in the Atlantic is similar to that in the Pacific. Localities having a biomass of 10 mg/m^2 are especially notable. In the abyss off Brazil, however, the biomass is practically nil. Now with the data on the quantitative distribution of the bottom fauna in all oceans, it is possible to estimate its total biomass more precisely as about ten tons.

The regularity of the quantitative distribution of the oceanic plankton and benthos is somewhat different (Fig. 4). I have attempted to show this by a simple diagram of the quantitative distribution of the bottom fauna, chiefly offshore, but the zonation determining the distribution of planktonic organisms in the surface layers is largely latitudinal. Unfortunately, our data for the quantitative distribution (biomass) of oceanic plankton is insufficient for mapping all the oceans but the distribution of the biomass at several levels in the world oceans can now be demonstrated.*

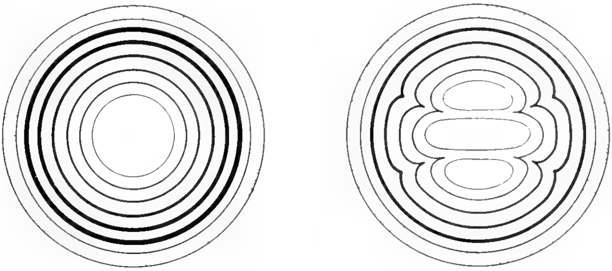


Fig. 4. Schematic representation of varied quantitative plankton and benthos distribution in the total ocean.

Fluctuations in the planktonic biomass are markedly less—they range from a few grams in coastal areas and decrease to a fraction of a milligram (0.17 mg/m^2) offshore in the ocean depths or fluctuations of ten thousand times. This shows that food for

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* The specimens collected by the *Lomonosov* in the Atlantic Ocean have not yet been charted.

plankton organisms is not derived from coastal areas and that it is not of primary importance.

With depth the amount of the biomass also decreases (Fig. 5). In various shallow-water areas and close inshore, the bottom-dwelling fauna fluctuates one thousand times and on the ocean bed only one hundred times. The plankton in the surface zone fluctuates four hundred times, but only five to eight times in the abyss. A thorough quantitative mapping of pelagic and of level-bottom communities of the ocean is important in furthering oceanographic knowledge. In ascertaining the regularity of the distribution and replacements of living organisms as well as the trophic relationships between them for a reliable estimate of the populations in the halosphere, these may serve as an indication of the physical processes and aid in our understanding of the role of living organisms in the chemical cycle in the ocean. All these phenomena should be expressed quantitatively or they lose their scientific or practical value.

It is well known that in recent years oceanologists in all countries have paid considerable attention to the ways in which radioactive fallout is distributed within the oceanic water masses and also the speed by which it occurs. Simultaneously, the form, rate, and scope of the oceanic contamination caused by radioactivity is also being investigated. It is quite obvious that the

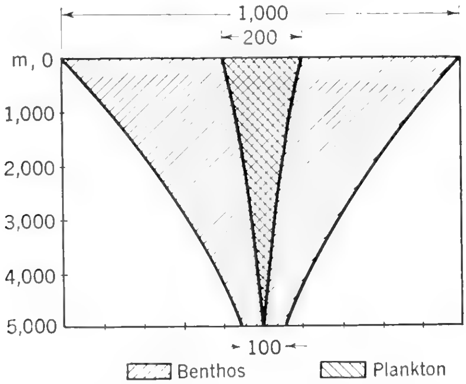

Fig. 5. The change of fluctuation rate of the benthos and plankton biomass with depth.

scientists' attention is being focused more and more on living organisms as one of the chief factors in the transfer and distribution of radioactivity throughout the water masses. Ketchum and Bowen (1958) write of "biological transport" and attempt to estimate this quantitatively and to compare it with the "physical transport." A term "biocirculation" has also been coined. It is evident that this phenomenon cannot be overlooked either as a means of transport or as an absorptive device. Most of the inert suspended materials move comparatively slowly, and bacterial and phytoplankton cells provide a huge adsorptive surface (Table II; Fig. 6). There is a considerable amount of material in suspension both living (bacteria, phytoplankton, and zooplankton) and inert (bioseston and abioseston). The quantitative determination of these seston groups provided the possibility for an evaluation of their part in adsorption and biocirculation (both vertically and horizontally).

TABLE II. Adsorptive Surface in Various Seston Groups in Distribution Zones of Middensity and Indices of Subsurface Biocirculation in a Column below 1 m^2 within Density Zones of Living Organisms

Seston Group				Column	
Abioseston per column 1000 m	Bacteria per column 900 m	Phytoplankton per column 100 m	Zooplankton per column 4000 m	Vertical (zoopl.)	Horizontal (fish)
10,000–40,000 m^2	400–500 m^2	0.5–2–5 up to 31 m^2	0.8–1.1 m^2	10,000–20,000 km/year	2.5–135 km/year

The mechanism for chemical equilibrium within the water masses is not well understood. Comparing data for the quantitative distribution of organisms and their chemical composition (Vinogradov, 1953) with the chemical composition of the bottom sediments, and with their accumulation rate indicated that it is possible (at least for several chemical components) to make fairly accurate formulas for the accumulation of certain substances on the bottom and their return to the water masses. These estimates can be obtained principally for $CaCO_3$ and SiO_2. For example, the

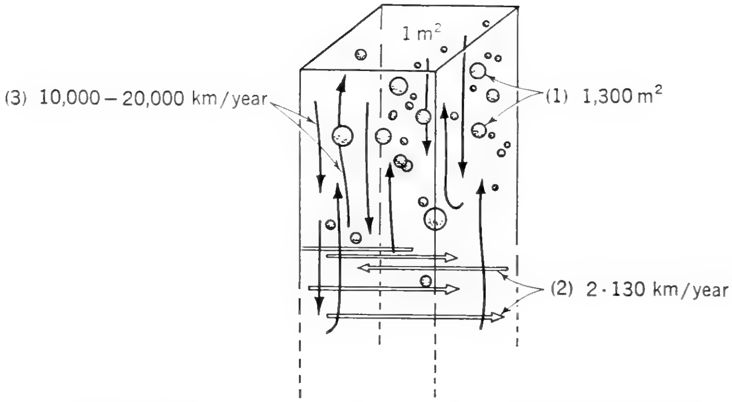

Fig. 6. A scheme of the adsorption system of seston and the vertical migration plankton and the horizontal migration of fishes beneath 1 m² of ocean surface in the mild zones characterized by mean life density.

bottom accumulation of $CaCO_3$ in the tropics from anthozoans should yield not less than 5×10^{11} tons per year. The annual accumulation of SiO_2 on the bottom of the Bering Sea is of the order of 8×10^7 tons. Calculations of this sort enable us to obtain certain quantitative characteristics of many aspects of the chemical balance in the ocean which can be compared with the data of paleochemistry. Hence, it is essential that quantitative investigations of the composition of various biological and biochemical processes in the ocean be developed and expanded.

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Turbulent Transport

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Turbulence versus Turbulent Transport

HOW often the word "turbulent" is used to mask ignorance of a fluid dynamical process! A casual inspection has revealed apparent disorder in space and time. The conclusion is that the process is a random one. "Turbulent transport," on the other hand, suggests that something has occurred as a consequence of the turbulence; hence, such turbulence must have a certain average order and cannot be completely random. I believe that almost all the turbulence encountered in nature is transporting something. In fact, I believe that the turbulence is there primarily to effect such transport.

In the fluid world the most obvious turbulent transports are of mass, momentum, and heat. Why does the geophysical fluid prefer turbulent transport to the molecular processes of transport seen in laboratory phenomena? The reason usually given is that the steady laminar flows of the laboratory are stable against arbitrary disturbances and return to their original configurations, but that large-scale flows are unstable to disturbances and break up into "eddies." Hence we may conclude that the resulting turbulence is the fluid's way of reestablishing its stability. Though turbulent may seem to many the very opposite of stable, fluids can and do achieve "statistical stability" by means of the turbulent transport of heat and momentum. One explanation of the statistical stability achieved by turbulent transport is that by redistributing heat and momentum the fluid reduces the energy sources of the instabilities which led to turbulence. However, any simple explanation of such a complicated process as statistical stability must be treated as suspect.

At the Woods Hole Oceanographic Institution I seek to isolate the simplest experimentally realizable types of turbulent transport which can be studied theoretically. In these controlled experiments one can hope to establish the range of validity of quantitative hypotheses concerning the field of motion. In this paper I shall (1) explore the possibility of isolating those turbulent processes in the sea which one might hope to treat theoretically, (2) explore some of the continuity relations which must exist between the separated turbulent processes, and (3) show that the more detailed mechanistic studies of the last decade support the inferred relations. In particular, I wish to paint an idealized picture of the North Atlantic circulation suggesting the various turbulent mechanisms which control the flow and to predict certain integrals of mass, heat, and momentum transport which one can compare both with observation and other theories.

The Turbulent Ocean versus an Idealized Ocean

Many different length scales characterize the many turbulent transport mechanisms of the sea. The momentum transport from air to sea produces both the smallest and the largest of these turbulent motions. This momentum transport, often called wind stress or wind friction, leads to turbulent wave fields on the small scale and turbulent fluctuations in the total southerly mass transports on the large scale. Two important turbulent heat transport processes with length scales between these wind-driven motions are the vertical convection of heat due to winter cooling of surface water and the Gulf Stream fragments or eddies which are an example of baroclinic turbulence due to horizontal temperature differences.

In his exploration of the density field of the sea, the oceanographer has found the one variable which least reflects the underlying turbulent dynamics. It was plausible that the relatively steady density structure would suggest a rationalization of the dynamics in terms of steady laminar-like flows. Interpreted as average flows, the laminar idealizations are both sound and illuminating. However, the structure and amplitude of these flows can be determined from the winds and surface heating only if we include in our analysis the turbulent transports of momentum and of heat. Unfortunately the length and time scales of this turbulence can be very large, for example the Gulf Stream fragment region, and here caution must be exercised in interpreting the average condition.

The idealizations of the North Atlantic density field and surface circulation given in Fig. 1 may amuse, but certainly will not shock, the practical oceanographer. He has become enured to the struggling theoretician and even will accept as a rough picture the two-layer ocean shown in pole to equator section on the right of this figure. The wind stress, τ, is responsible for driving the hot T_H surface layer south and west to form a strong boundary current which sweeps north to mix with cold T_C northern waters. However, not a single symbol or a single line on this drawing should be accepted except as a very crude integral of a fluid process.

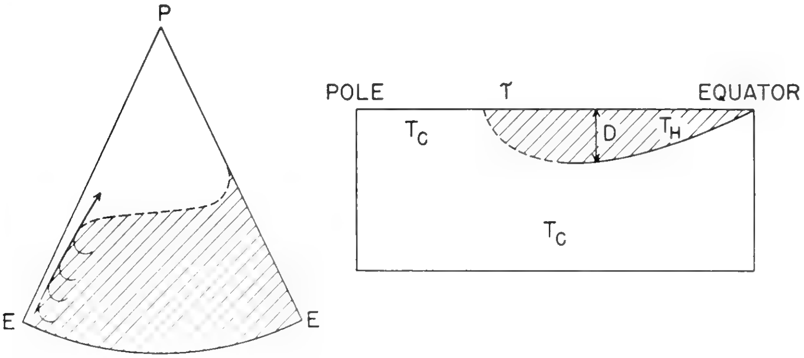


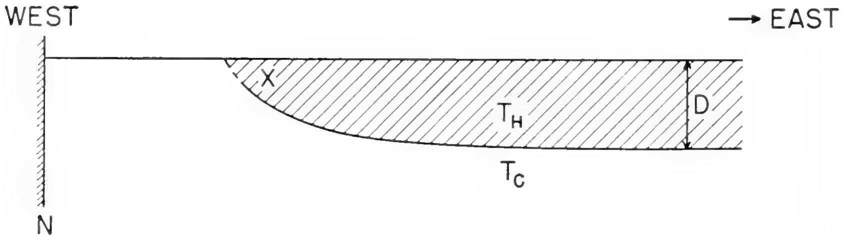
Fig. 1. An idealized North Atlantic Ocean.

Isolating Several Turbulent Processes

The vector τ is given as a number and a direction, yet it stands for the fascinating process by which a turbulent wind transfers momentum through the wave-whipped surface to generate a net mass transport at right angles to τ. The temperature T_H hides much of marine meteorology. If we understood the complicated turbulent processes of evaporation and cumulus convection over the tropical oceans, we might be able to predict T_H. It is the basic quantity defining the energy source for atmospheric motions and for the thermal circulations of the sea. The temperature T_C is the consequence of both energy radiation to space and turbulent convection into cold winter winds. Complicated as it is, the T_C process is perhaps the least complicated of those I shall mention. The depth D of this two-layer ocean is an idealization of the two-layering process. We shall discover that D is related to the balance struck by cold water ascending from the depths and the turbulent transport of heat down from the surface. The arrowhead part of our boundary current indicates the region in which the Gulf Stream first breaks into turbulent fragments and mixes with the surrounding colder water. These fragments will play the dominant role in the dynamics along the entire northern boundary of the upper layer.

Continuity Requirements

To give this statistically steady idealization pedagogic value the quantitative consequences of the conservation of mass, momentum, and heat must be discovered. In Fig. 2 appears a west to east section of a two-layer Gulf Stream at latitudes south of the region of fragmentation. Perhaps one of the more satisfying products of the last decade of study of western boundary currents is the confirmation of their almost frictionless and geostrophic character. In his book, *The Gulf Stream*, Stommel (1958) of the Woods Hole Oceanographic Institution gives a lucid description of the dynamics of this flow. It is strange that although the southern part of the Gulf Stream is the most steady and organized flow in the ocean the northern part generates the most dramatic oceanic turbulence.



$$\underbrace{T_S = \frac{1}{\beta}\int_W^E (\nabla \times \tau)}_{} \equiv \underbrace{T_N = \frac{g\alpha(T_H - T_C)}{2f} D^2}_{}$$

Fig. 2. An idealized two-layer boundary current.

The mathematical relation on the right shows the total transport of mass to the north in the upper layer (T_N) for a geostrophic flow of arbitrary depth profile. In this relation g is the acceleration of gravity, α the coefficient of thermal expansion of water, and f is the Coriolis parameter. For continuity in our upper layer T_N must equal the total mass transport to the south induced by the wind stress over the entire layer. The mathematical relation on the left is Sverdrup's (1947) famous deduction relating the southerly mass transport to the wind stress and to β, the variation of f with latitude.

However, the idealization requires that this Gulf Stream, or at least a significant fraction of it, mix with the colder waters of the north. Therefore conservation of mass requires that cold water be reincorporated into the upper layer. The baroclinic energy sources for this Gulf Stream fragmentation require that, on the average, warm water rise and colder water sink. Hence it is unlikely that more than a fraction of the cold water will be reincorporated into the upper layer by horizontal transfer at the northern boundary of the upper layer. The alternative is the reincorporation of cold water into the upper layer by a general ascent under the whole tropical ocean. The conservation of heat requires that this reincorporated cold water be warmed by a heat flow down from the surface and also that the warm Gulf Stream fragments in the northern sea be cooled by a heat flow up through the surface to the atmosphere and to space.

The integral consequences of these continuity requirements are:

$$H = \frac{T_N \Delta T,}{A} \quad \Delta T \equiv (T_H - T_C), \quad W = \frac{T_N}{A}$$

$$H = W\Delta T \equiv K\frac{\Delta T}{D}$$

$$K = DW$$

The total kinematic heat flux to the north is $T_N\Delta T$. As this is lost to the upper layer, it must be resupplied by an average local heat flux H equals to $T_N\Delta T/A$ down from the tropical surface, where A is the area of the upper layer and ΔT is equal to $T_H - T_C$. The average vertical velocity of the cold water reincorporated into the upper layer is T_N/A. Therefore, H equals $W\Delta T$.

The two-layering process suggested here represents a balance struck by the ascending cold water and the turbulent descent of heat. In the last few years many different turbulent mechanisms have been suggested as responsible for this vertical heat flux. Three such mechanisms are given. Their variety indicates the almost complete lack of knowledge of the actual oceanic process.

First, the energy to drive a convective heat flux in a vertically stable fluid could come from the horizontal flows induced by the wind. If this is so, the total mixing should be related to the wind speed and the density contrast in the sea. Hence, one would expect seasonal variations in the vertical temperature structure where the winds show marked seasonal variation and little seasonal variation in regions where the winds are steady.

A second energy source for convection could be internal waves. It appears that internal waves would have to break to effectively mix. There is plenty of tidal energy available to drive internal waves but no one has yet explored the fashion in which this energy might be made available to the convection.

A third convective mechanism is that one responsible for the reincorporation of the seasonal thermocline. This appears to be due to winter cooling of the surface waters. In fact the long persistence of the warmed surface layer produced in summer suggests that other mixing processes are quite weak. However, parts of the tropical ocean have almost no seasonal thermocline and here convection must be due to other causes.

These different processes for the vertical flux of heat would have motions with quite different characteristic space and time scales, yet whatever the actual process may be, the continuity requirements of our idealized circulation prescribe the total amount of heat which must be convected. In order to establish how much larger than the microscopic heat transport the effective turbulent transport must be, we may define an average turbulent coefficient K as equal to $HD/\Delta T$. I suggest no other function for an "eddy conductivity" than this integral estimate. For example, use of such a constant K in a dynamical treatment of the seasonal mixing process is clearly of little value.

To determine H, D, W, and K we must know ΔT, T_S, and A. An estimate of ΔT from the observations is approximately 15°C.

An estimate of the total southerly transport from the wind stress is $T_S = 3.10^7$ m^3/sec. An estimate of the area of the upper layer is approximately $1.5 \cdot 10^7$ km^2. With these values the idealized ocean must transport $4.5 \cdot 10^{14}$ cal/sec to the north. This is comparable to the heat transported north by the atmosphere. The depth of the upper layer determined by ΔT and this T_S is 700 m. The average vertical velocity W approximately equals $2 \cdot 10^{-4}$ cm/sec, suggesting a yearly incorporation of 60 m of cold water into the upper layer. The required K approximately equals 14 cm^2/sec and suggests that the vertical turbulent transport of heat must be at least a thousand times as effective as the molecular transfer of heat.

Relation of Idealization to Mechanistic Studies

The idealization of this highly simplified North Atlantic ocean has two explicit purposes. The first purpose is to exhibit the role of turbulent transport processes in controlling the structure and amplitude of a wind and thermal-driven circulation. The second purpose is to provide a setting in which to mention several recent theoretical achievements in the study of detailed dynamics of parts of the ocean. In attempting to fulfill the first purpose I have listed the several turbulent mechanisms which are essential to sustain an ocean-like circulation. Many less essential turbulent transports were not mentioned and certain exist in the real ocean. I believe that we can effectively study most of these turbulent phenomena in isolation. For example, let us study just vertical heat transport, then just horizontal momentum transport. In this fashion we may construct an adequate language of inquiry and analysis for the assembly of separate transports into an operating ocean. However, an operating ocean is not necessarily the real ocean. We must be increasingly critical of both our old preconceptions and our new deductions in the observational and experimental tests.

Related to our idealization is the dynamical study of Stommel (1956) on the concentration of the southward moving cold water to the west of the ocean basin. The experimental confirmation of this deep current by Swallow and Worthington (1957) represents one of the few victories of deductive oceanography. A second study by Robinson and Stommel (1959) treats the two-layering process of the tropical ocean with the powerful boundary layer techniques of modern fluid dynamics. By requiring a turbulent heat flux of the size found here they determined from the equations of motion the depth D, the vertical velocity, and, in part, the variation of the depth D with latitude. The last appears to be a more kinematical than dynamical consequence of the motion. The mean motion of their fluid system can be generated by wind stress, internal thermal circulation, or both. The internal thermal circulation due to gradients in the surface temperature was not included in my idealization. However, such circulation may play a significant subsidiary role in horizontal mixing of the upper tropical waters. It has been suggested that such horizontal mixing may be responsible for the amazing constancy of the ratio D/f between 10° N and 35° N. In fact, if the north-south horizontal transfer of heat in the tropical ocean is comparable to the total heat flux HA found earlier, it would make the average value of W even more representative of the actual local vertical velocity.

I have not mentioned nor included in the idealization the role of salinity in modifying the circulation. I have not mentioned the important role of the internal wave as a transporter of momentum and as a degrader of energy. Yet it is perhaps this mechanism which decelerates the rotation of the earth-moon system. However, in conclusion, I shall mention that even the simple geometric quantity A, the area of the warm layer of the ocean, is an ever changing turbulent process whose dynamics must one day be explored.

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Pelagic Sediments

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THE vast extent of pelagic deposits, covering about 70 per cent of the ocean floor, thus about half of the earth, makes them of obvious importance to all earth science. A record, more nearly complete than elsewhere, reflecting many major events of earth history will surely be found through examination of pelagic sediments, especially with their penetration to greater depths. Obviously only a few aspects of the subject, from a geological viewpoint, may be considered in this paper.

Pelagic sediments seems a useful term although it is not easily defined, as there is a considerable variety of such sediments and, naturally, gradations from pelagic to other sediments. Derivation from *pelagos* only implies "of the open ocean," but it has been restricted in usage by differentiating such sediments as the hemipelagic sediments bordering major land masses. All the pelagic (eupelagic) sediments, whether largely of plankton remains or fine inorganic particles, have certain distinctive characteristics to reflect their environment of accumulation. Pelagic sediment is precipitated and/or settled from the overlying ocean waters of regions where rates of accumulation are slow enough to cause little change in the great volume of circulating bottom waters, and the little sediment thus accumulates, and normally remains, in a highly oxidized state. This is reflected in their composition and more obviously in the colors of red, brown, and buff. Even the more nearly white oozes, composed largely of plankton remains, show only small parts of the sediment, and these are beneath the

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surface, of green gray color from locally developed reducing conditions.

Some deep-sea or abyssal deposits, even though distant from continents or islands, seem properly excluded from the pelagic type. These include the glacial-marine, and the turbidity current deposits. These are more rapidly accumulated and thus less oxidized, and are likewise more similar to the hemipelagic and continental sediments in lithology, mineralogy, and thus in chemical composition.

Some of the deposits composed largely of the remains of plankton may also be excluded, not only because these were accumulated near or even on the continents, but also normally accumulate more rapidly and lack the characteristic of highly oxidized components. These might be termed planktonic deposits except for confusion of such with those of the typical pelagic deposits composed largely of plankton remains. It is, however, this distinct kind of deposit of plankton remains, lacking the highly oxidized character of pelagic deposits, such as some in the Gulf of California, which form the usual and perhaps only plankton accumulations known in the ancient strata on the continents. Their much greater rate of accumulation is commonly reflected in their thickness relative to probable time, and rather than being highly oxidized like pelagic sediments, these are normally high in organic matter content. A thick deposit, for the amount of upper Eocene time, is known as the Oceanic formation in Barbados, B.W.I., because of the abundance and variety of marine planktonic remains, including many Radiolaria. It lacks, however, the pelagic sediment feature of slow accumulation with the highly oxidized character of the iron minerals. The reported red clay in this formation has proved to be limited only to weathering of some present day exposures of the rocks.

Depth of water, though normally great, is not a factor of particular significance for pelagic deposits, as *Globigerina* ooze on guyots and banks shows the typical characteristics of pelagic sediments even where accumulated at hundreds rather than thousands of meters. Here it commonly shows better than average sorting in grain size, but a similar relation of sorting to topography is apparent in some pelagic sediments at great depths.

The most distinctive chemical and other characters of pelagic deposits thus seem related primarily to their slow accumulation and the resulting approach to chemical equilibrium with the normal open ocean bottom water environment. Even the comparatively rapid pelagic accumulation of some *Globigerinà* ooze in the equatorial Pacific, at rates of several centimeters per thousand years, results in only the oxidized minerals of iron and tetravalent manganese. The gray diatomaceous sediments of the subarctic Pacific are not highly oxidized. Menard (1955, p. 240) has indicated, however, that this is largely glacial-marine and turbidity current deposition. Diatom remains are a distinctly minor element, and as indicated, these deposits also lack the slow accumulation and other features of typical pelagic deposits.

Many of the more interesting discoveries and advances in knowledge of pelagic sediments are coming from geochemistry, and the stratigraphic evidence of former conditions that is indicated in core samples. Much regarding the surface sediments, however, remains little changed from the pioneer work of Murray and Renard (1891). Not only is the *Challenger* volume on deep-sea deposits a great compilation of data, but much of the interpretations seem confirmed.

The classification and most of the terms of Murray and Renard, though not entirely satisfactory, are sufficiently descriptive and well known not to require time to discuss the original or any modified definitions here. Even their map of distribution covering most of the earth's surface presented much of the major features indicated on the map from Sverdrup *et al.* (1946, p. 975, Fig. 253). It will be indicated that though the pelagic clay includes great areas with different colors and other characters, the old term "red clay" still seems not entirely inappropriate as a general term, in that it implies the highly oxidized character of all pelagic clays.

The great volume of calcareous deposits in the oceans presents problems that have been much discussed. The present rate of supply of calcium from the rivers is sufficient to double the large amount in the oceans in about one million years if no calcium were removed, and Revelle and Fairbridge (1957, p. 244) calculated this should result in deposition equivalent to 0.66 g of carbonate per square centimeter per thousand years for an area equal to the whole ocean floor. A large but indeterminate part of this accumulates in hemipelagic deposits and locally, as in coral atolls, but most of it must go into the pelagic calcareous ooze. The noncalcareous "red" clay, where solution results in no carbonate accumulation, covers about one-third of the total area, and thus would not radically change the above estimate on rate for the areas of calcium carbonate accumulation. This rate based on influx from rivers corresponds approximately with the 1 cm per thousand years for *Globigerina* ooze accumulation, indicated by Kuenen (1950, p. 383).

The great excess of calcium carbonate deposits in the rocks of the continents, over the percentage to be expected from the original igneous rock sources, cannot represent a segregation there, through dominance of shallow water deposition of the calcium carbonate, if the present great percentage of calcareous deposition in the deep-sea persisted through much of the earth's history known in the sedimentary rocks.

This enigma is evident in all the attempts at a geochemical balance of the elements eroded from igneous rocks and accumulated in all sediments and ocean water. The various estimates and results cannot be summarized here. Results from various approaches and assumptions led Kuenen (1950, p. 389) to conclude that the present large segregation of calcium carbonate in pelagic sediments may have begun in Cretaceous time, with the advent of the planktonic Foraminifera. The coccoliths and other very small calcareous remains of planktonic algae appear to have been a more important carbonate component than the Foraminifera until late in the time since the Cretaceous. Present evidence, however, does not preclude the possibility that all such calcareous plankton were unimportant before the Cretaceous. This interpretation is inviting as it could account for a great dominance of shallow water deposition of the calcium carbonate, by the benthonic organisms, and perhaps inorganically, in pre-Cretaceous time.

An attempt at a geochemical balance by Goldberg and Arrhenius (1958, p. 207) resulted in a much smaller total volume of the noncalcareous pelagic clays than that of Kuenen's computations, but the same problem of a long-term lack of balance for calcium carbonate deposition is again evident in their results.

The following observations of the present extent and rate of accumulation of pelagic calcium carbonate deposits seem to offer little help to this problem, but rather emphasize it more.

The shells and their fragments from pelagic Foraminifera, including *Globigerina*, clearly form most of the calcium carbonate of modern pelagic deposits. The tiny coccoliths from certain planktonic algae form a minor part of the present day calcareous deposits. No inorganic crystals or other nonskeletal calcium carbonate is found in pelagic sediments.

Figure 1*a* shows an electron microscope photograph of the fine part of such sediment, which consists of coccoliths of a few microns that are also discernible with a light microscope, and their recognizable debris in the finer fraction of less than 0.1 micron, with no inorganic carbonate.

Figure 1*b* shows a core (Ch 40) of pelagic sediment of Miocene age, with only about 10 cm of Quaternary cover and small amounts of the upper part carried down in borings from benthonic organisms. The Miocene clay grades down into coccolith ooze. The shorter core (Ch 17), at different scale, is of Oligocene age that has almost no later sediment cover. It is a coccolith ooze with a few per cent of pelagic Foraminifera, and more than 80% calcium carbonate. A small manganese nodule is evident, and the dark upper surface is largely a surface residue from dissolution of the calcium carbonate. It contains the same Radiolaria as in the lower sediment, but here it is mixed with a few Recent ones.

Figure 2*a* shows the abundant calcareous remains known as discoasters and some of the larger coccoliths from the core of Oligocene age. The discoasters, though generally associated in occurrence with coccoliths, are only questionably related, as they are now largely or entirely extinct forms. These average about 10 microns in size. Figure 2*b* shows another such assemblage of Miocene age.

Much recent data by Bradshaw (1959, p. 53, Fig. 37) on the living populations of pelagic Foraminifera in the Pacific provide information here interpreted in terms of present rates of accumulation on the sea floor. Figure 3 shows his summarized total population values, with the highest productivity areas indicating more than 100 specimens per cubic meter of water. A large part of the subarctic Pacific is known to have high plankton productivity but it is perhaps surprising that this is indicated also for the calcareous Foraminifera. His data, however, indicate that the number of species is small here.

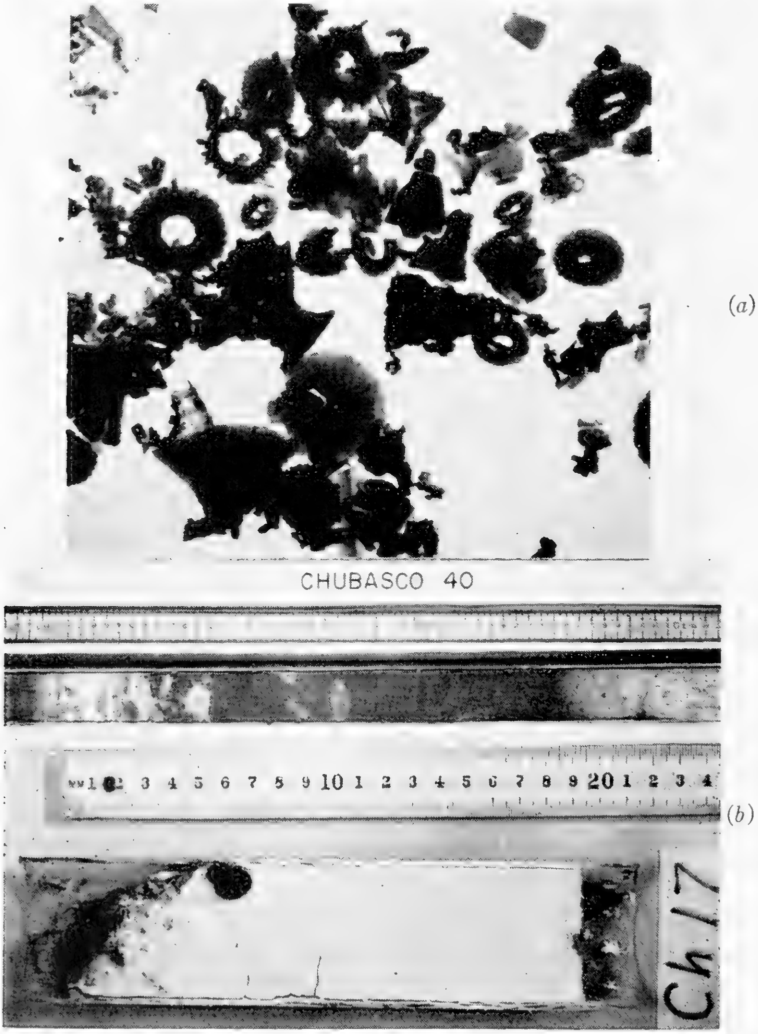

Fig. 1. (*a*) An electron microscope photograph of coccoliths and fragments of them from calcareous ooze of Quaternary age (× 3,000). (*b*) Core Ch. 40 of Miocene age, except upper 10 cm (at left) of Quaternary age. Core Ch. 17 is an Oligocene calcareous ooze. Different scales indicated.

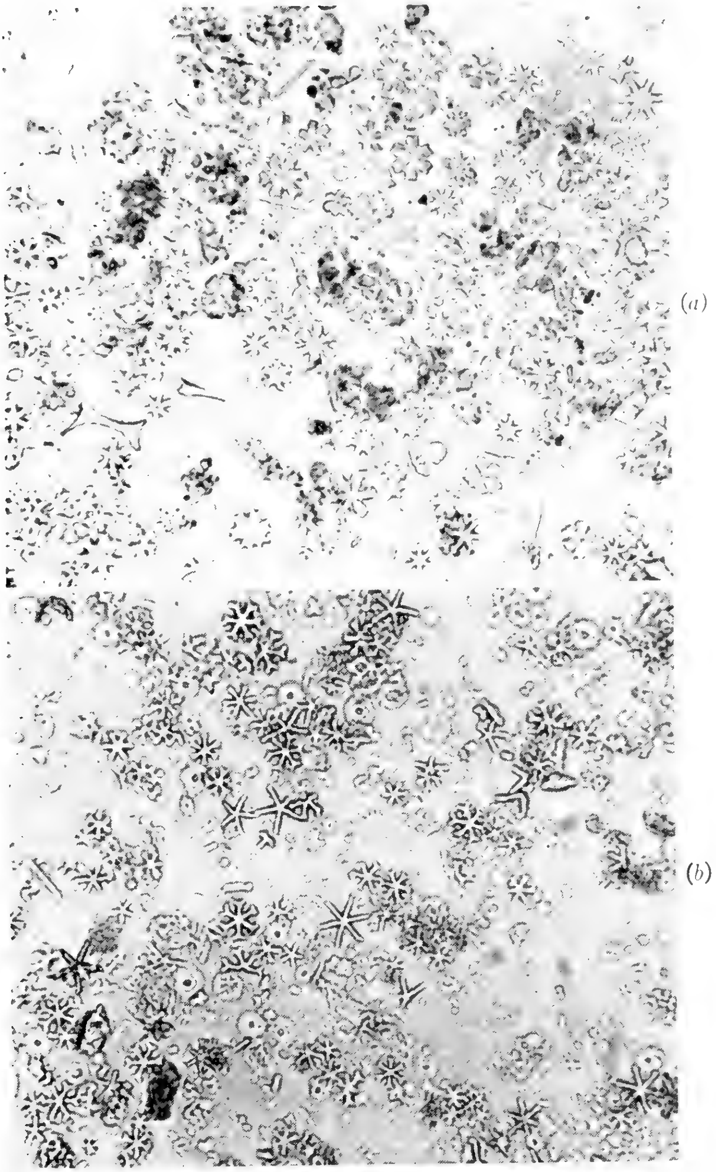

Fig. 2. (*a*) Constituents of core sample of Oligocene age, showing many discoasters (× 450). (*b*) Discoasters and coccoliths from core sample of Miocene age (× 450).

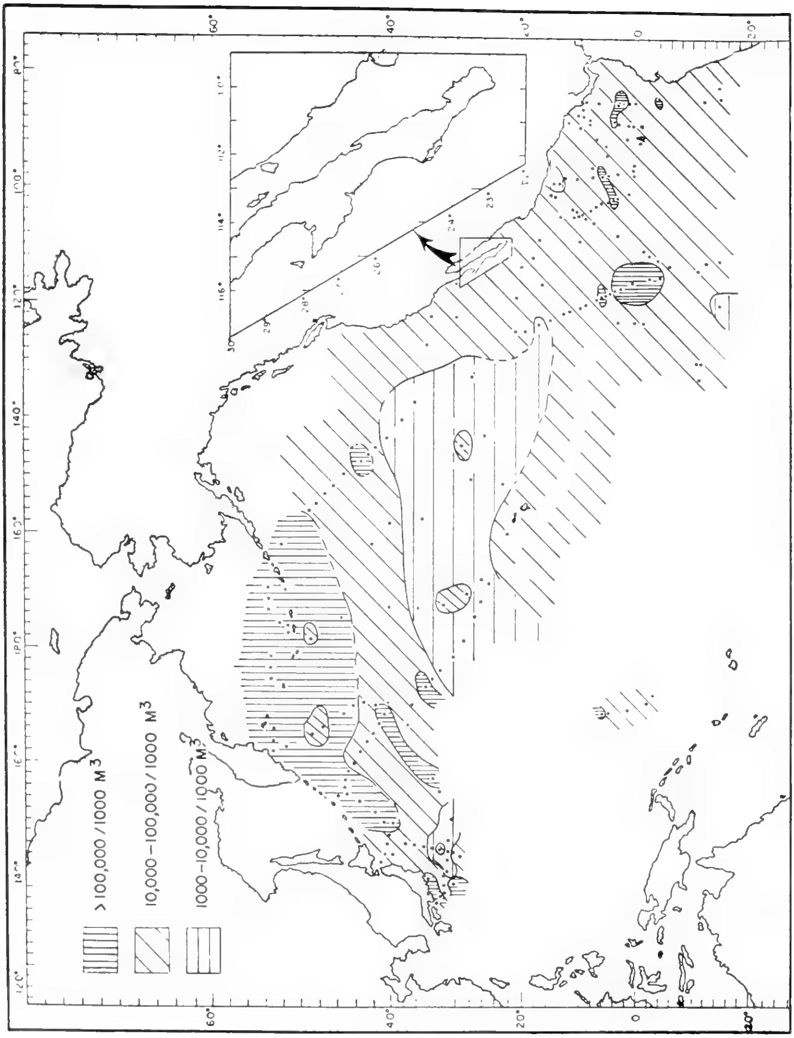

Fig. 3. Distribution of planktonic Foraminifera in the North Pacific (Bradshaw, 1959).

In the more productive areas, 100 specimens per cubic meter is near Bradshaw's average down to a depth of 100 m, with rapid decrease at greater depths. This would approximate 10,000 for the total water column above a square meter of ocean floor. With a life cycle or residence time of about one year probable, this indicates deposition of one calcareous test per square centimeter of the bottom per year. This rate would approximate only 1 mm of *Globigerina* ooze per thousand years.

This rate of accumulation would be only one-tenth of the 1 cm per thousand years indicated from other evidence as near an average rate of post-Tertiary accumulation, and expectable from rate of supply of calcium by rivers. The approximate balance indicated by saturated waters should be maintained in major part by *Globigerina* ooze deposition. Even smaller rates would be indicated for most of the North Pacific showing the much smaller standing crop. Solution with no net accumulation occurs over much of this region of 5000 m or more depth.

Some recent data by Bé (1959, p. 80, Table 2) indicates much smaller populations of planktonic Foraminifera in the North Atlantic than Bradshaw shows in the Pacific Ocean. The reverse would be expected from rates of post-Pleistocene accumulation in the two oceans. Differences and inadequacies of sampling methods would not seem to account for the difference that exceeds an order of magnitude of ten. Perhaps the residence time or life cycle is much less than one year, and the accumulation rate thus greater, but this would not affect the great difference indicated for the two oceans. Need for additional data on this problem is evident.

Over large areas of the ocean, such as that in the equatorial Pacific, calcareous tests (dominantly planktonic Foraminifera) constitute up to more than 80 per cent of the sediment. In this belt of high productivity in the equatorial current and countercurrents, the diatom and radiolarian remains commonly form 10% or more. The clay and other inorganic particles are less than 10%. This and following considerations indicate that in the more productive areas of the ocean the remains of calcareous organisms have accumulated at rates up to nearly 10 times that of other pelagic sediments.

Arrhenius' study (1952, p. 192) of the Swedish deep-sea cores in the equatorial belt shows a thickness up to more than 10 m of the Quaternary *Globigerina* ooze, with the minor amount of clay accumulation. His extrapolation from a rate determined by carbon-14 suggests an average rate near 1 cm per thousand years for this calcium carbonate accumulation. He indicates a distinctly lower Recent rate of carbonate accumulation than the average of Quaternary time for the equatorial belt of high productivity.

In contrast to some 10 m of Quaternary *Globigerina* ooze accumulation in the equatorial Pacific, the thickness for non-calcareous clay of this age to the north seems to average near 1 m, and rates here averaging 1 mm per thousand years from ionium-thorium ratios by Goldberg are in agreement. The fine clay suspension in the ocean waters that Kuenen termed the lutite veil is not apt to accumulate at uniform rates everywhere, especially in regions with marked differences in bottom topography and water movement. As measured by TiO_2 percentage, however, its accumulation does not seem to vary by more than a factor of 2 in the equatorial Pacific region and seems to serve as a very rough approximation for relative rates of accumulation over larger regions. Despite all the approximations and uncertainties, it seems evident from the area and rates of calcium carbonate accumulation that its total volume dominates that of Quaternary pelagic accumulations.

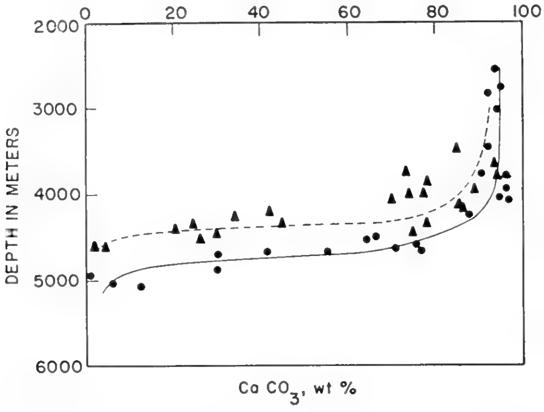

Fig. 4. Pelagic surface samples of the Pacific. – – – – Across Tuamotu Archipelago, 10°–27° S Lat, 128°–147° W Long. ——— Across east Pacific rise at approximately 45° S Lat (*Downwind* expedition).

Murray and Renard (1891), and all since, have recognized that solution of calcium carbonate is important on the deeper parts of the ocean floor, and is a factor in the decreasing carbonate content below depths of about 4000 m. What may be called a compensation condition, where supply does not exceed the solution, and thus with no net accumulation of calcium carbonate, includes obvious factors other than depth and rate of supply. Data presented here, however, appear to indicate that factors related to a rather narrow depth difference are more important than has previously been indicated, and largely control the pattern of carbonate percentages in pelagic sediments. Conditions related with marked deviations to unusually great depths, or rates of supply, or other factors will be apparent, but the depth of compensation remains surprisingly near limits between 4000 and 5000 m. The sharp decrease in $CaCO_2$ and compensation depth appears even more limited, within a range of about 500 m in localized regions where depth differences are greater than differences in the other factors. This poses a problem on the solubility conditions in the bottom waters that a depth below 4000 to 5000 m appears so important.

Figure 4 shows $CaCO_3$ per cent plotted against depth in meters for an area near 10–27° S Lat in the Pacific. The curve shows a

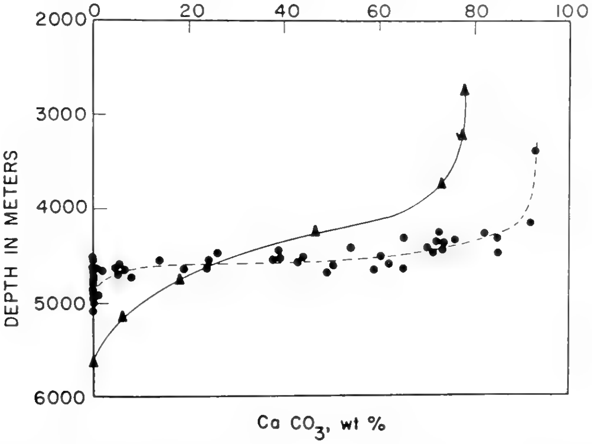

Fig. 5. Calcium carbonate versus depth of the Pacific. – – – – Central equatorial Pacific, 15° N to 5° S Lat, 120°–135° W Long. ——— Average for 500-meter intervals from all available data for top of core samples.

sharp decrease with depth, and a compensation depth near 4500 m. The lower curve is from a more southern area, between latitudes 40° and 50° S, where the compensation depth is greater (near 5000 m), and comparable with that common in the Atlantic Ocean.

Figure 5 represents an area at the north edge of the Pacific equatorial belt of high productivity and carbonate deposition. The carbonate percentage is here controlled more largely by the abrupt change northward in carbonate supply from the counter-current belt of very high productivity, and with little change in depth of water. Even here, however, the depth relation is also indicated, with a compensation depth near 4700 m. The other curve is an average of all available samples from the Pacific, affected by all the variable factors, but nevertheless showing a marked change between 4000 and 5000 m. The points are based on averages for all samples between 500-m intervals.

Figure 6 shows the distribution of calcium carbonate from all available data for the central and eastern Pacific, and its relation to the depth contours of 4000 and 5000 m. Despite the inadequate control on both, the relation of carbonate content and depth is apparent in the southern Pacific. It would be closer if additional depth contours, such as 4500 m, were shown, as indicated by individual core depths. Most of the North Pacific is below depths of 4000 m, but factors other than depth are apparent here. Productivity of calcareous plankton is relatively low over large areas, including part of that of less than 4000 m depth to the southwest of Mexico. Rapid clastic accumulation and high organic matter content have been indicated for the large region off Alaska. Increased supply of CO_2 to the bottom waters thus seems probable, and may influence the compensation depth above 4000 m here.

Statements commonly imply that the solution largely occurs during the descent of calcareous shells to great depth. This time, however, is insignificant compared with that possible on the ocean floor, with the slow rates of accumulation. Foraminiferal tests settle at rates requiring only a few days to reach 5000 m depth, but might remain near the sediment-water interface for hundreds of years in areas of no net accumulation of carbonate. Coccoliths, averaging 5 microns, would settle much more slowly (requiring

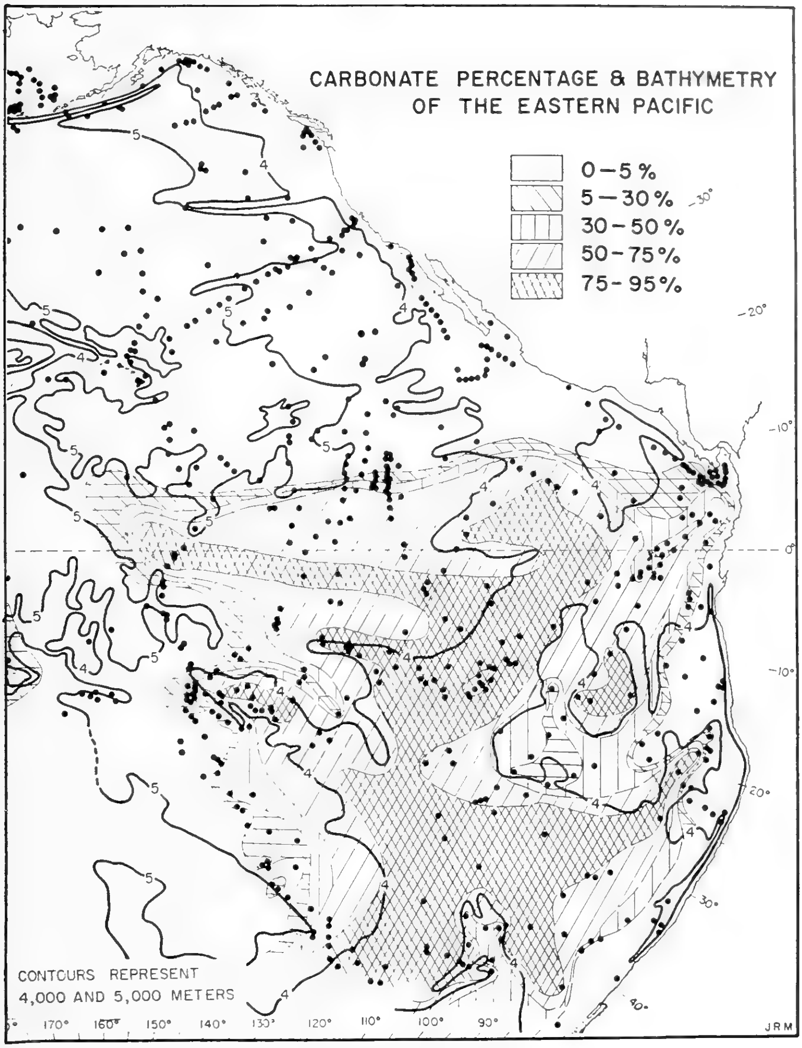

Fig. 6. Carbonate percentage and bathymetry of the eastern Pacific (data compiled by Mr. Donald Lynn).

more than 10 years), yet these normally reach the bottom, and accumulate with the Foraminifera above the compensation depth. Coccoliths are lacking only near and below this compensation depth, where any remains of Foraminifera consist only of fragments of the thicker shell parts.

The cold bottom waters of polar origin are known to be relatively high in carbon dioxide, and thus are able to dissolve more of the calcium carbonate. It seems improbable, however, that temperature stratification in the waters could be so marked that this factor alone could account for the sharp limits of the compensation depth that have been indicated. Most present consideration of increased solution from hydrostatic pressure does not suggest it as a major factor. It may seem worth additional investigation, however, for with pressures below about 4000 m becoming rather critical, it could explain the sharp limits indicated for the compensation depth.

Other interesting but quantitatively minor biogenous deposits can be mentioned only briefly.

As indicated, the diatomaceous belt of the North Pacific contains a minor part of diatoms, and lacks the features characteristic of pelagic deposits. Diatoms appear to average little more than 10 per cent of this sediment, as indicated by x-ray determinations of Goldberg, after converting the opaline silica of the diatoms to cristobalite by heating. Samples from the Antarctic belt are more highly diatomaceous, and in part, at least, show the more oxidized character of typical pelagic sediments.

The small size and shape of diatoms results in settling rates approximating 50 years or more to reach the bottom, and the more delicate ones are dissolved before reaching the ocean floor. Lateral distribution by currents appears to be less extensive, however, than has been suggested, as indicated by Fig. 7. These unpublished data from Kanaya indicate a few of the characteristic species, among more cosmopolitan ones, that are not mixed in the bottom sediment throughout the Pacific. The indicated distribution from north to south in the Pacific is only from the few samples studied to date.

The skeletal remains of Radiolaria are a conspicuous element of some pelagic sediment, though seldom amounting to more than about 10 per cent even in the so-called radiolarian ooze. Accumulation appears greatest in the equatorial belt of generally high productivity, but they dominate the biogenous component only in the north edge of this belt where solution of calcium carbonate has increased their proportion. Their value in age assignments has

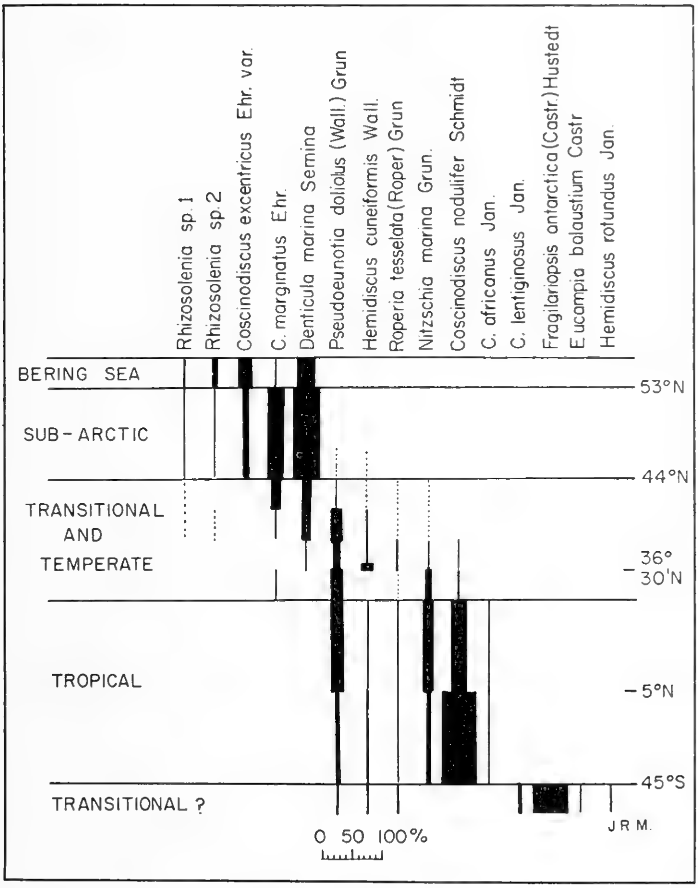

Fig. 7. Distribution of diatoms in Pacific sediments, few selected species (preliminary data from T. Kanaya, unpublished).

been demonstrated by Riedel (1959), especially in sediments where few other fossils have been preserved. Solution of the opaline remains occurs even within the sediment, however, under some conditions. (See Fig. 8*b*.)

Debris from pelagic fish is quite a minor element, but accounts for the relatively high phosphorus content of pelagic sediments. The scales are generally dissolved, but teeth and larger amounts of small skeletal fragments accumulate in the sediment. This material is of particular interest because of the surprising amounts of certain elements concentrated from the bottom waters. These include several per cent of rare earths, abnormal amounts of zinc, copper, tin, and lead, and radioactive elements such as thorium (Arrhenius *et al.*, 1957). Figure 8*a* shows the tracks, in a photographic emulsion, of alpha particles from such a fish fragment. The brown color from organic components in the fish fragments is gradually lost with time in the oxidizing environment, and appears more related to rate of sediment accumulation or burial than to age. This material in Tertiary pelagic deposits has generally lost the brown color, although this is not the case for many Tertiary and older sediments from environments less oxidizing and more rapidly accumulated than in the pelagic one.

The pelagic (red) clay still poses many problems, such as the proportion derived from pyroclastics and the various other sources. Much of this information may come with more reliable methods and knowledge on clay mineralogy. Occurring over the vast areas with water depths of 4000–5000 m or more, it contains little calcareous material, but commonly includes less than 1% of small rhombs of dolomite, apparently formed within the sediment as indicated by Correns (1939, p. 385) for the Atlantic Ocean. Even the opal tests of plankton, especially of the delicate diatoms, tend to be dissolved in the slowly accumulated clay, and at depth within it. Figure 8*b* shows in thin section one of the radiolarian tests that has been largely dissolved within Tertiary sediment at 8 m below the top of a core.

Although pelagic clay is generally highly oxidized, and high in manganese, there is much variation in some features, with a marked difference between some large regions. The pelagic clay of the South Pacific might seem a type area, as it is here most distant from major land sources of sediment. Accumulation in the area seems slower than average from several characters, including the exceptionally high manganese content with the resulting dark brown color. Goldberg's ionium-thorium ratios also indicate the slow rate, of about ½ mm per thousand years. Pyroclastic material of andesitic to basaltic composition is particularly abundant here, though the original glass component has completely disappeared, except in local areas of more rapid accumulation near some volcanic islands. The hydrated glass, with the iron converted to ferric state, known as palagonite is common. One of the zeolite

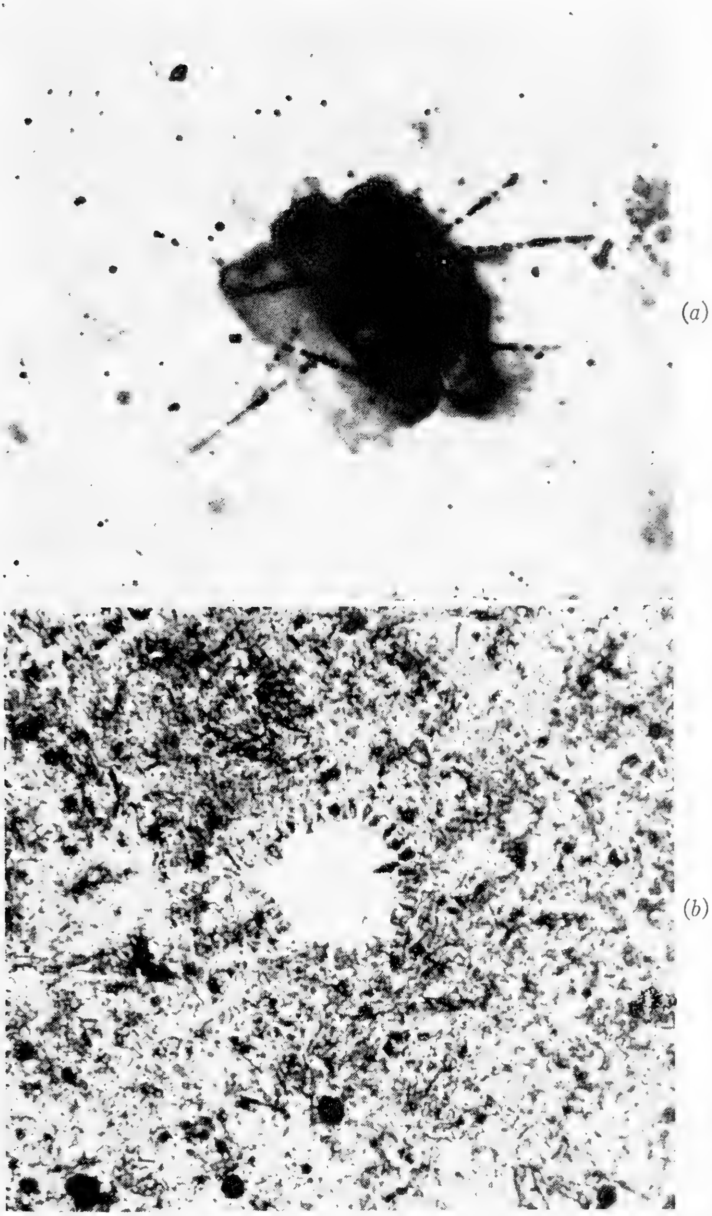

Fig. 8. (*a*) Small fragment of fish skeleton showing alpha tracks in the emulsion (Reprinted with permission from *Researches in Geochemistry*, P. H. Abelson, Editor, p. 17, John Wiley & Sons, New York, 1959.) (*b*) Partially dissolved radiolarian skeleton in thin section of Tertiary sediment at 8 m below top of core, Capricorn 49 BP (× 200).

minerals, phillipsite, is also especially common in the South Pacific, and forms up to nearly 50% of some pelagic clay. Figure 9*a* shows the abundant phillipsite crystals unseparated from other fine sediment. The associations, especially where the phillipsite is in concentric bands with palagonite around incompletely altered basaltic glass, support the conclusion of Murray and Renard (1891, pp. 405–411) that the phillipsite was derived from the alteration of pyroclastics. Arrhenius is investigating interesting features of phillipsite which include high concentration of certain elements, such as the radioactive ones that show alpha emissions like that illustrated from the fish debris (Fig. 8*a*). Derivation of such elements from the bottom water, however, does not preclude derivation of the essential constituents of phillipsite from alteration of the pyroclastics by the bottom water. Such derivation of the silica, alumina, calcium, and perhaps the potassium, rather than directly from the ocean water, seems probable, as the common association of zeolites with altered pyroclastics, even in nonmarine waters, is well known.

The pelagic clay of the North Pacific shows differences from that of the South Pacific that may be related in part to closer proximity to land sources, and other factors to be mentioned, which have increased the rate of accumulation. Goldberg's determinations here show rates between 1 and 2 mm per thousand years here compared with rates of ½ mm in the South Pacific. The iron and especially manganese content is distinctly less than in the South Pacific. Pyroclastics and their alteration products are also less important here, probably in part because more diluted with other material. The sparsely disseminated volcanic shards of alkalic glass are unaltered in the near surface sediment, and indicate much less susceptibility to alteration than a basaltic glass.

The quartz content, as particles averaging less than 10 microns, is relatively high, especially near 30° N Lat in the Pacific, and Rex and Goldberg (1958) relate these high percentages to dust fallout, mostly from the jet stream circling the globe near this latitude. Menard (1955, p. 240) indicated that turbidity current deposition is important in the northwest Pacific, and perhaps the finest of the suspended particles from this may also contribute

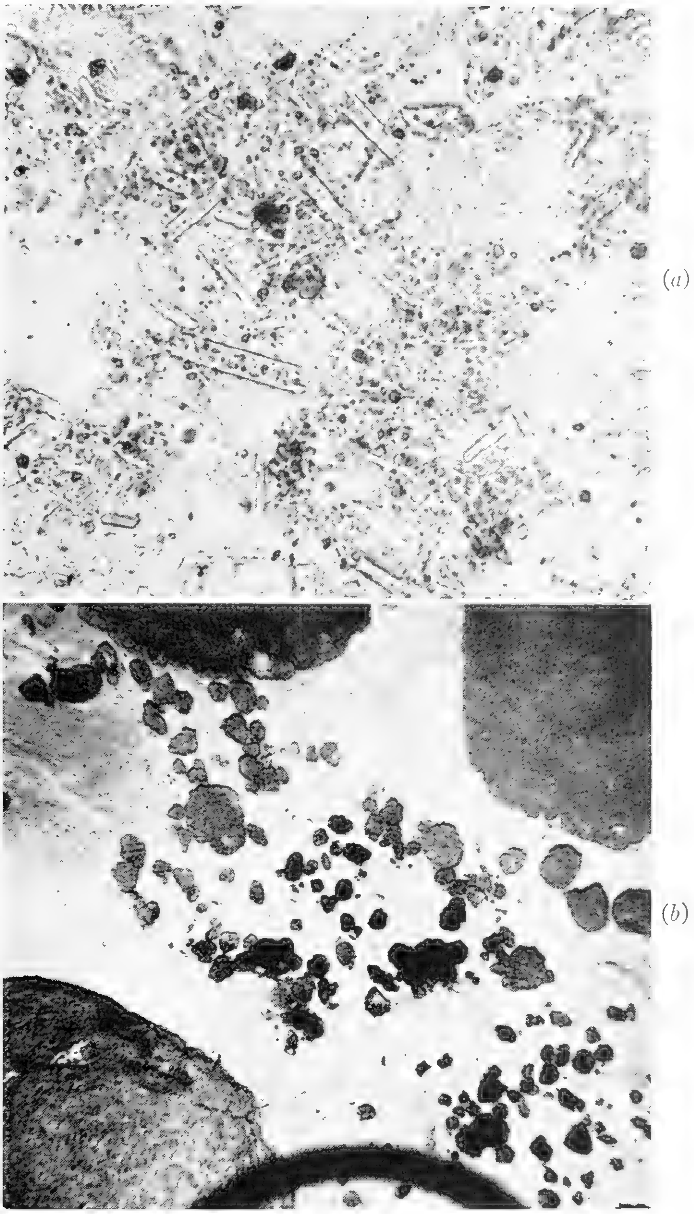

Fig. 9. (*a*) Crystals of phillipsite (elongate laths), unseparated from other particles of pelagic clay at 114 cm in core, Midpac 3 (× 200). (*b*) Manganese nodules at depth of 4560 m in southwestern Pacific (area about 6 m square). (Photo DWP–11 from Menard and Shipek, 1958.)

more to the pelagic sediments in the North Pacific than in the South Pacific.

Sources and rate of pelagic clay accumulation in the North Pacific thus seem more similar to those of the Atlantic Ocean than in the South Pacific, and these differences seem clearly reflected in the color and other features of the pelagic clays of the two regions.

A distinct discontinuity between this surface clay of the North Pacific and an underlying clay much like that in the South Pacific is encountered in many cores at depths of about 3 to less than 1 m, with the upper bed thinner on topographic highs. The upper clay shows the usual character of modern pelagic sediments of this region, including any remains of the plankton preserved, and is doubtless all of Quaternary age. The clay below the marked discontinuity is commonly dark brown, and similar in this color and other features to the surface clay of the South Pacific. Goldberg and Arrhenius (1958, p. 203) show the chemical composition of the lower clay is also more like that of the South Pacific.

All this sediment below the marked change is probably of Tertiary age, as indicated where evidence from fossils is adequate. Some of the differences in sources of sediment and rates of its accumulation that result in the marked differences of modern clay in the North Pacific from that beneath it, may thus indicate certain post-Tertiary influences greater in the North Pacific than in the South Pacific where no such difference in the later clay is evident. Goldberg has indicated that the windborne fine-grain quartz is much less common below the discontinuity. Both this, and any possible contributions from areas of turbidity current deposition in the northwest Pacific, might be more conspicuous with advent of the glacial times.

The great segregation of manganese in pelagic sediments presents many problems, but only one may be considered here. Vast amounts are disseminated as fine particles or micronodules in the slowly accumulated pelagic clay. Very great amounts are also obvious in the large nodules over large areas of the ocean floor

Menard and Shipek (1958) have estimated, from such photographs as shown in Fig. 9*b* and many dredge and core samples, that these nodules cover from one-fourth to one-half of large areas of the floor, especially in the southwest Pacific. Their estimates of amounts are so great that, including the considerable percentage of cobalt and nickel, eventual recovery and utilization seem possible.

Coring generally indicates that finely disseminated manganese is in greater amounts in underlying sediments (of pre-Quaternary age in part, at least) than near the surface. The coring also indicates, however, that the nodules are more concentrated at the present sediment surface. A suggestion is offered that may account, in part at least, for the exceptional amounts occurring as nodules on the present ocean floor.

The large accretions as nodules from the low percentage of manganese in solution in ocean water are obviously in regions of slow sediment accumulation. Although the average of sediment accumulation has been indicated as now more rapid than in the pre-Quaternary, there is considerable evidence that the character and rates are now less uniform over the ocean floor than in the pre-Quaternary.

Water temperatures were higher and more uniform in the Tertiary, from data of Emiliani (1954) and others. This should result in a more uniform areal distribution of the supply of calcium carbonate from surface waters. The greater compensation depth with warmer water would greatly reduce the areas of solution of carbonate below this depth. Less cold polar bottom water with its higher carbon dioxide content, would also have less influence on the differences in solution related to topography and depth than followed the advent of glacial times. Sorting and grain size differences related to topography also appear greater in the recent sediments, and suggest stronger bottom water motion than that usual in Tertiary time. This also results in differences of accumulation rate between areas.

Summarizing this too brief consideration of evidence, it suggests that the high proportion of manganese accumulation as large nodules is now abnormal because rates of sediment accumulation, though now greater than average, also show much greater differences between areas. Those present day areas of relatively slow accumulation may thus permit deposition of more of the manganese as large nodules, rather than as the disseminated micronodules that are in larger proportion in the Tertiary.

Many interesting, even though minor, components of pelagic sediments cannot be mentioned here, such as the cosmic spherules discussed by Fredriksson (1959), and many geochemical and other aspects must be omitted.

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Geochemistry of Radioactive Elements in the Ocean and the Chronology of Deep-Sea Sediments

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MODERN techniques make it possible to obtain cores of sediment of from 10 to 20 m in length from the ocean bottom. Owing to the slow and continual sedimentation present in deep oceans, these columns generally represent complete archives of the Pleistocene era (approximately a million years). In ocean zones of very slow or discontinuous sedimentation, these columns may penetrate even into Tertiary sediments of several tens of millions of years of age.

During this Congress, several speakers, among them Dr. Gustaf Arrhenius, have emphasized the large quantity of important information to be gained from a study of such sediments. Some examples of this information would include: climatic variations deduced from paleontological studies (Foraminifera, Radiolaria) or by Urey's isotopic oxygen method; the rate of sedimentation in the ocean deeps; the oceanic biological productivity; polar drift; volcanic activity on the earth surface; variations in the chemical composition of the ocean; variations in oceanic circulation; variations in the flux of cosmic radiation; and the rate of accumulation of micrometeorites and cosmic dust. In all these cases, one particular problem arises, that of fixing a time scale, in order to date in an absolute manner the observed phenomena.

Admittedly, the only valid methods of chronology of geological phenomena at present are those based on radioactive disintegration. These methods have proved their worth in the field of classical geology, and especially in the geology of the pre-Cambrian era, where they have been used to measure ages of from some tens of millions of years up to some billions of years. In the chronology of the oceanic sediments presently available, the ages to be measured are much younger—from several thousands up to several millions of years. For reasons that will be stated later, we do not as yet possess as great a number of well-proved radioactive methods to measure intervals of time of this order as for longer ones. I should like to describe briefly the present state of research in this field and the outlook for progress in the near future.

Four names representing three important stages in our progress in this field should be mentioned here: Joly, who as early as 1908 had discovered the high radium content of pelagic clays; Hans Pettersson, who in 1937 suggested the precipitation of ionium in the ocean and who instigated a fruitful European collaboration in the field of oceanic radiochemistry; and Piggot and Urry, who from 1940 to 1950 laid the foundations of radioactive methods for the chronology of pelagic sediments.

Principles of Radioactive Methods of Age Determination

Let us briefly recall the well known principles for the radioactive methods in geological chronology. A group of radioactive atoms can serve as a geological chronometer because it undergoes an irreversible evolution, an evolution which progresses at a constant rate, independent of physical or chemical conditions (or at least of terrestrial conditions). This evolution is their spontaneous transformation into stable atoms.

Let R be a radioactive nuclide with λ the probability that this nuclide will spontaneously disintegrate in unit time. This λ is a constant characteristic of every nuclear species and is independent of the chemical or physical conditions of the medium. By disintegration, R will be transformed, either directly or indirectly, into a stable nuclide S. Should the transformation be indirect, that is, by way of other radioactive nuclides, R forms a *radioactive family*.

Let N_0 be the number of atoms of R present at time t_0. This number will decrease exponentially with time owing to the disintegration of the atoms of R. The number of atoms, N, remaining after the passage of time t from t_0 is given by the well-known formula:

$$N = N_0 \cdot e^{-\lambda t}$$

Figure 1 shows this function. N/N_0 is generally expressed, not as a function of t, but as a function of $T = 0.693/\lambda$, where T is the half life and represents the time in which the number of atoms R remaining has diminished by 50 per cent from the original number N_0.

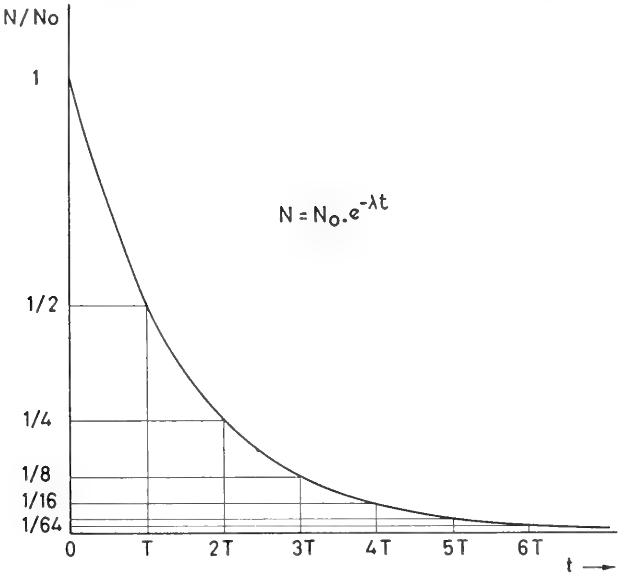


Fig. 1. Law of radioactive decay. The unit of time is taken as the half life.

Consider now a natural system (for example a mineral, a rock, or a living being), which is completely formed at time t_0 and which stops all chemical exchange with the surrounding medium. Let us suppose that at the instant t_0 the imagined system includes a number N_0 of radioactive atoms of the type R. At any moment later than t_0, the age of this system is the amount of time that has passed from the moment that all chemical exchange or, more precisely, all exchange of atoms of type R, or its ascendants or its descendants, with the external medium had ceased.

If N_0 is the number of atoms of R at time t_0, and N is the number now present, the age t of the system may be calculated from the fundamental equation:

$$N/N_0 = e^{-\lambda t} \tag{1}$$

Let us note that a knowledge of N alone does not suffice for a calculation of t. In other words, if we have a system containing a radioactive isotope R and know only the amount of this isotope present in the system, we cannot calculate the age of the system. We need to possess further information prior to doing this.

Practically all methods of measurement could be included into one or the other of the three types;

1. Either N_0 or only N/N_0 is known. Generally, N/N_0 is known because R has one, or several, stable isotopes, and its isotopic abundance in the external medium is known at the time of separation of the system. The age of the system can be calculated directly from equation (1). The carbon-14 method is of this type.

2. R is transformed, either directly, or indirectly into a stable nuclide, S. The ratio of the concentrations of R and S actually present in the system allows the age to be calculated from the equation:

$$S/R = (e^{\lambda t} - 1)$$

This is valid only under certain conditions, conditions which we shall not discuss here. This type of method includes most of the classical methods: Pb/U, Sr/Rb, A/K, and He/U.

3. R is a member of a radioactive family, and is transformed into another radioactive nuclide R′, with a shorter life. If, at the moment of formation, t_0, of the system, only R is included in it and no R′, the ratio R′/R will increase from its initial value of zero up to its maximum value upon attainment of radioactive equilibrium between R and R′. Since the actual ratio R′/R is known, the age t of the system may be deduced by using the equation:

$$R'/R = (1 - e^{-\lambda t})$$

on condition that $T \gg T'$. The method Io/U is of this type.

Some particularly interesting applications exist because two of the three radioactive families have isotopes of the same element at their head: U^{238} and U^{235}. It is possible, in such cases, to calculate the age of the system by applying one of the methods described above, when only the ratio of the concentrations of two members of the two families, independently of the absolute value of their concentrations is known. We shall cite an example of this type later.

The Serviceable Radionuclides

The curves in Figs. 1 and 2 show that, in order to date a par-

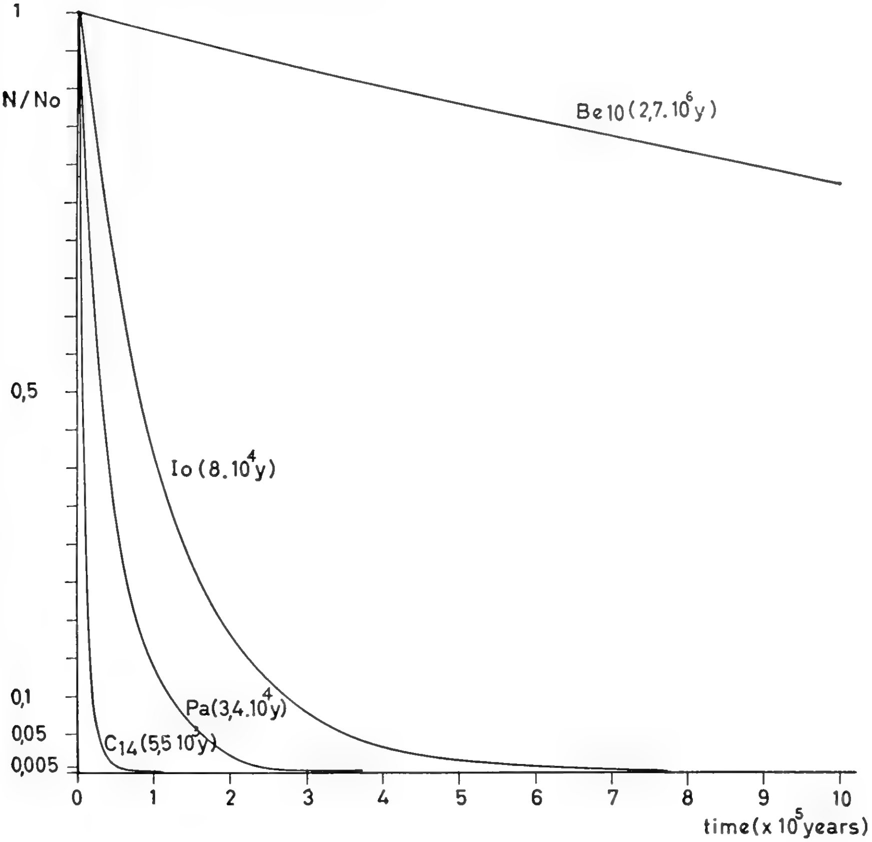


Fig. 2. Decay curves of radioactive nuclides used for dating pelagic sediments (back to ~ 10^7 years).

ticular phenomenon, the method employed must be based on a radionuclide which has a half time T of the same order as the age t to be determined. If $t \gg T$, the number of atoms of R remaining in the system becomes too small to be detected. If $t \ll T$, the decrease in the number of atoms of R will be very small, and will lie within the limits of the experimental error.

The ages which present an interest in this field lie between a few thousand and a few million years. Radioactive nuclides with half lives of this order, short with respect to the age of the earth, are found in nature, and may be classified in two groups, according to their origins: (1) the members of the three radioactive families, and (2) radioactive nuclides formed by the interaction of cosmic rays with constituents of the atmosphere or of the lithosphere.

Among the first group we notice three nuclides with half lives lying between 10^3 and 10^6 years, namely (1) in the U^{238} family, radium-226 (T = 1600 years), (2) ionium (Th^{230}) (T = 80,000 years), in the U^{235} family, (3) protactinium-231 (T = 34,000 years).

The longest half life among the members of the thorium family is that of mesothorium-1 (Ra^{228}) which is 6.7 years.

The second group contains a large number of short-lived nuclides. The only two which have a half life longer than 10^3 years and exist in measurable amounts in the ocean or its sediments, are carbon-14 (T = 5500 years) and beryllium-10 ($T = 2.5 \times 10^6$ years).

Let us briefly recall what we know of the geochemistry of these radioisotopes in the ocean and in its sediments.

Natural Radioactive Nuclides in the Ocean

Table I summarizes our present-day knowledge of the concentrations of radioactive nuclides in the ocean. It is noteworthy that by far the largest part of the ocean's radioactivity is due to the presence of K^{40}.

The nuclides tritium, carbon-14, and beryllium-10, formed by cosmic ray action, are discussed in recent reviews by Begemann and Libby (1957), Giletti *et al.* (1958), Broecker (p. 301), Merrill *et al.* (1958), and Peters (1957). The other radioactive nuclides are

TABLE I. Natural Radioactive Nuclides Present in the Ocean[a]

Nuclide	Half life, years	Concentration, g/ml	Isotopic abundance, %	Disintegrations, per sec and per ml
H^3	1.2×10^1	3.2×10^{-21} [b]	1.0×10^{-16}	1.1×10^{-6} β
C^{14}	5.5×10^3	3.1×10^{-17} [b]	1.3×10^{-10}	5.2×10^{-6} β
Be^{10}	2.7×10^6	1×10^{-16}		7×10^{-8} β
K^{40}	1.3×10^9	4.5×10^{-8}	1.2×10^{-2}	1.1×10^{-2} $\beta+\gamma$
Rb^{87}	5.0×10^{10}	3.4×10^{-8}	27.8	1.0×10^{-4} β
U^{238}	4.5×10^9	2×10^{-9}	99.3	2.5×10^{-5} α
Th^{230} (Io)	8.0×10^4	6×10^{-16}	$>3 \times 10^{-3}$	4×10^{-7} α
Ra^{226}	1.6×10^3	8×10^{-17}	~ 100	2.9×10^{-6} α
U^{235}	7.1×10^8	1.4×10^{-11}	0.7	1.1×10^{-6} α
Pa^{231}	3.4×10^4	5×10^{-17}	~ 100	8×10^{-8} α
Th^{227} (RdAc)		7×10^{-23}		8×10^{-8} α
Th^{232}	1.4×10^{10}	2×10^{-11}	~ 100	8×10^{-8} α
Th^{228} (RdTh)	1.9	4.0×10^{-21}		1.2×10^{-7} α
Ra^{228} (MsTh)	6.7	1.4×10^{-20}	$\sim 1 \times 10^{-2}$	1.2×10^{-7} β

[a] Concentrations in surface waters in 1953, prior to thermonuclear tests.

[b] For references to literature see text.

discussed in greater detail in articles by Holland and Kulp (1954), Koczy *et al.* (1957), and Suess (1958).

Let us now consider the nuclides of the three radioactive families, and their radioactive equilibrium states, these equilibrium states being the basis for the methods of chronology of the sediments. We must remember that any two nuclides belonging to the same family undergo the same number of disintegrations per second when the family is in radioactive equilibrium. Column 4 of Table I permits a rapid check of the equilibrium state.

The earliest measurements of uranium in the ocean were carried out by Hernegger (1933) and later by Hernegger and Karlik (1935). Their results subsequently were confirmed by a number of other authors. The majority of reported results indicate concentrations of between 1×10^{-9} and 3×10^{-9} g/ml; the accepted average value is 2×10^{-9} g/ml.

Measurements on radium were carried out by two independent groups, that of Evans (Evans *et al.*, 1938) and that of Pettersson (Føyn *et al.*, 1939). A large number of determinations was carried

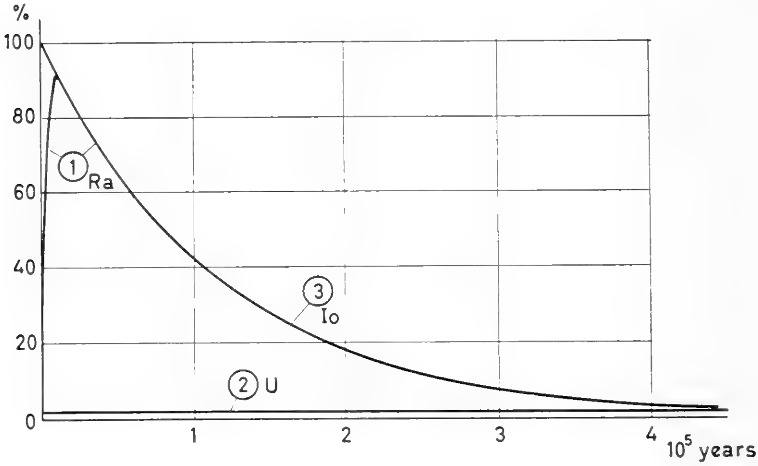


Fig. 3. Distribution of the activities of radium (1), uranium (2), and ionium (3) with respect to the age of the sediment layers, assuming the following ideal conditions: (*a*) the ionium content of each layer of a given core was constant at the moment of its deposition, and exceeded the equilibrium value with uranium by a factor of 50; (*b*) neither the radium nor the ionium diffuses after deposition of the sediment; (*c*) the uranium content is constant throughout the various layers.

out by the Swedish expedition of the *Albatross* (Koczy, 1956) headed by H. Pettersson. The concentration of radium appears to vary more widely than that of uranium, with values from 0.3 to 3×10^{-16} g/ml, the mean value being taken as 0.8×10^{-16} g/ml (Koczy, 1956). These early results pointed out a very important fact, namely that the radium in the ocean is not in equilibrium with its parents, U^{238}. It will be noticed (Table I) that, in fact, the number of disintegrations of radium per milliliter of water is of the order of 10% of that of U^{238}.

As early as 1937, Pettersson suggested that this situation could be ascribed to the precipitation, not of radium itself, but of its parent, ionium (Th^{230}). The first direct measurements carried out on ionium and other isotopes of thorium by Koczy *et al.* (1957) confirmed this hypothesis. These measurements have since been repeated by Sackett *et al.* (1958), using more representative samples, and their work confirmed the former.

Table I permits the following conclusions to be drawn with respect to the nuclides of the three radioactive families present in the ocean:

1. The members of the three families are present in a very low concentration in the ocean, much lower than in the earth's crust.
2. The ratio of the concentration of Th/U is exceptionally low. This ratio is less than 0.01 in the ocean, while it is of the order of 3 in rocks. This is a geochemical characteristic of the ocean, as was emphasized by Pettersson (1937).
3. The radioactive equilibria of the three families are completely dislocated. If we call $R_{A/B}$ the ratio of the specific activities of two members A and B of the same family, we find the following situations existent in the ocean (it must be remembered that if A and B are in equilibrium, $R_{A/B} = 1$):

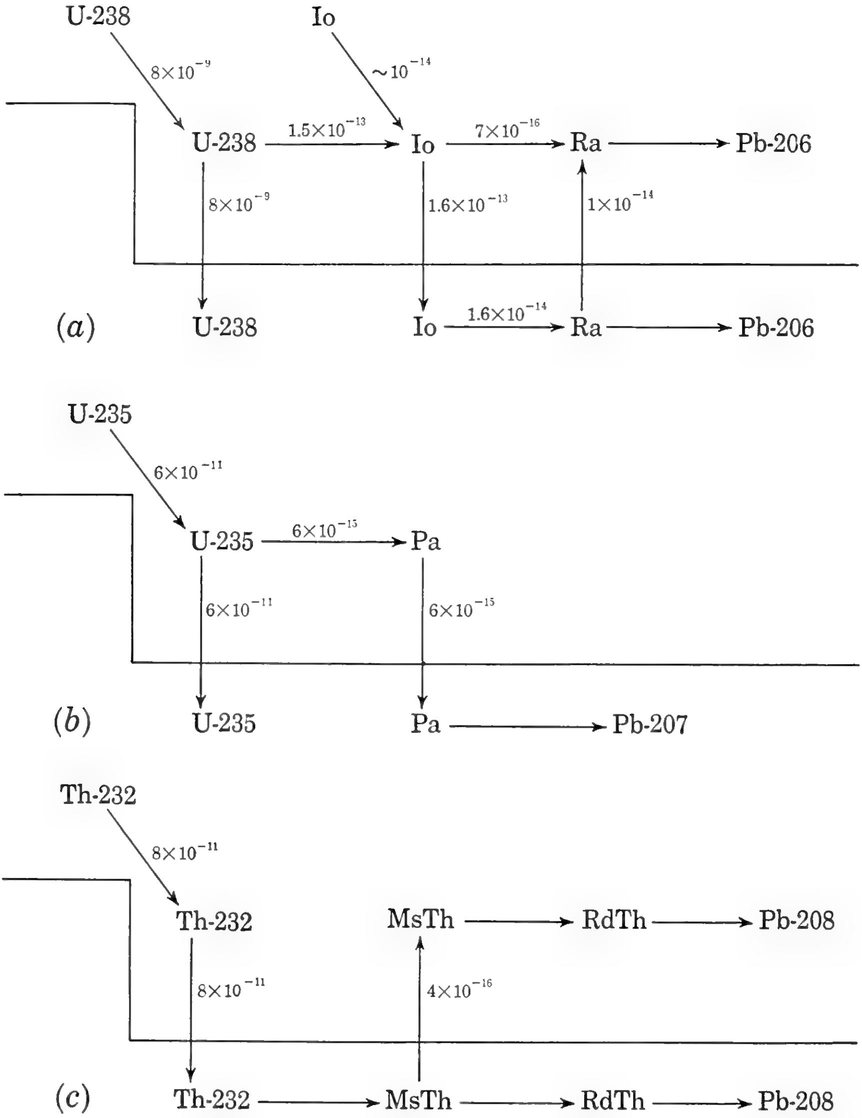
$R_{\mathrm{Io}/238} < 0.02$ $R_{\mathrm{Pa}/\mathrm{U}235} < 0.1$

$R_{\mathrm{Ra}/\mathrm{Io}} \sim 6$ $R_{\mathrm{MsTh}/\mathrm{Th}} \geqslant 4$

The ionium and the protactinium produced by the disintegration of U^{238} and of U^{235} have practically disappeared. This indicates that they have precipitated to the floor of the ocean in a time which is short compared to their half life. On the other hand, the two isotopes Ra and MsTh are in excess with respect to their respective parents Io and Th. We have interpreted this as due to the redissolution into the ocean, of Ra and MsTh formed in the sediments (Koczy *et al.*, 1957).

This situation, if confirmed, would present interesting possibilities for studies of oceanic circulation, complementing those opened by tritium and carbon-14. Radium possesses two advantages over C^{14} in that its half life of 1600 years is more adaptable to the scale of time of oceanic circulation and also in that it (radium) is liberated from the ocean floor, whereas C^{14} is introduced at the surface.

Thus, mesothorium, having a short half life (7 years) would practically disappear not far from the bottom. Its detection could be utilized to identify bodies of water that had been recently in contact with the sediments on the floor, or to measure horizontal currents leaving the continental shelf or passing in the neighborhood of suboceanic ridges.



Geochemical balance of the nuclides of three radioactive families in the ocean. The contributions are expressed in grams per square centimeter per year (Koczy, 1956; Koczy *et al.*, 1957).

↘ Contribution by rivers
→ Loss due to radioactive disintegration
↓ Loss due to precipitation on the floor
↑ Contribution by dissolution of the ocean floor

Radioactive Nuclides Present in Sediments

We shall confine ourselves to the question of recent pelagic sediments covering the floor of ocean deeps where the rate of sedimentation is extremely slow. Offshore epicontinental sediments, being essentially formed of detrital materials, normally have a composition which simply reflects that of the continental rocks from which they originate. In the case of pelagic sediments we would expect to find a situation complementary to that of the ocean. In other words, we would expect to find in excess over the radioactive equilibrium, the nuclides of the three radioactive families, which have a lower than equilibrium concentration in the ocean.

The earliest measurements of radium were carried out by Joly in 1908 on pelagic clays brought back by the *Challenger* expedition. They indicated a very high radium content, between ten and fifty times that of ordinary granitic rocks. These measurements have since been confirmed by Pettersson and by other authors. The origin of this high content was not, however, as easily agreed upon. Pettersson, in 1937, suggested that this excess radium was due to the presence of ionium, coprecipitated with ferric hydroxide. Piggot and Urry (1942a,b) showed that the distribution of radium in the depths of the sediment cores corresponded to that postulated by Pettersson's hypothesis. They based a method of chronology of the sediments on this, by indirectly determining the ionium by way of the radium present. The basic assumption of their method was that the radium, produced in sediments by disintegration of ionium, remained where it was, and did not migrate. This assumption appeared to be of rather doubtful value when differences in the chemical properties of radium and ionium are taken into account.

The numerous measurements carried out by Kröll (1953–1955) on the sediment cores brought back by the Swedish expedition on the *Albatross*, led by Pettersson, complicated the question even further. Kröll observed very irregular distributions of radium, which appeared to be incompatible with the simple model proposed by Piggot and Urry. A possible explanation for these irregularities

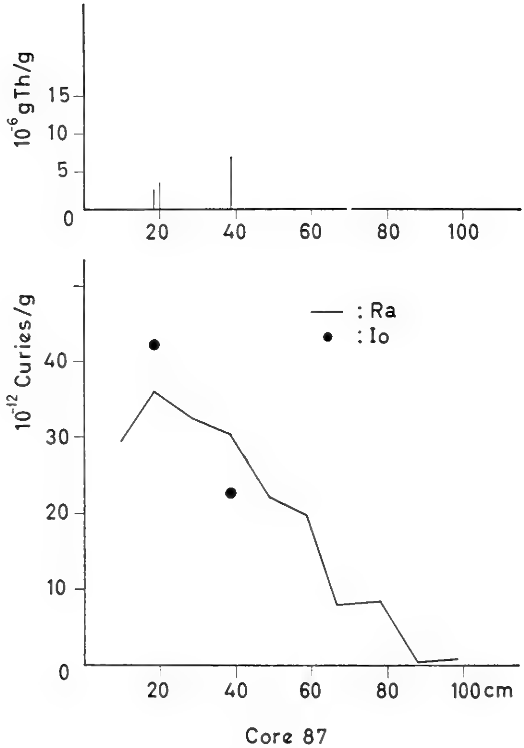


Fig. 4. Measurements on radioactive nuclides from Pacific clay core 87 of the Swedish deep-sea expedition 1947–1948. The graph shows the activities of the following nuclides plotted against depth in the core: radium (Kröll, 1955); ionium (Picciotto and Poulaert, unpublished). At top is shown the thorium content of selected layers in the core (Picciotto and Wilgain, 1954).

appeared to be due to a migration of the radium rather than to an irregular distribution of ionium.

The only way to resolve the problem was to measure directly the ionium as well as the radium in the same samples. In 1952, under the stimulus of Pettersson, a program of radioactive measurements on Pacific sediment cores brought back by the *Albatross* expedition, with European cooperation, was started. The radium was measured by Kröll at Göteborg; the uranium in Vienna by Hecht and his collaborators (Hahofer and Hecht, 1954); the ionium, thorium, and protactinium were measured, for the

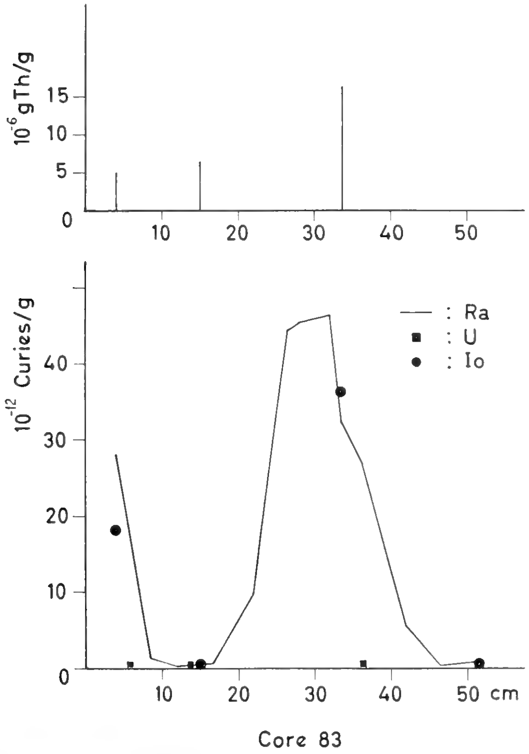


Fig. 5. Measurements on radioactive nuclides from Pacific clay core 83 of the Swedish deep-sea expedition, 1947–1948. Graph shows activities of the following nuclides plotted against depth in core: radium (Kröll, 1955); uranium (Hahofer and Hecht, 1954); ionium (Picciotto and Poulaert, unpublished). At top is shown the thorium content of selected layers in the core (Picciotto and Wilgain, 1954).

first time, in Brussels by methods which had been specially developed for this problem (Isaac and Picciotto, 1953; Picciotto and Wilgain, 1954; Hirschberg, 1954). Figures 4–6 show typical results.

A similar series of measurements has since been carried out in the U.S.S.R. by Baranov and Kuzmina (1958) on sediments of the northwest Pacific and of the Antarctic sector of the Indian Ocean.

All these results are still very dispersed, and a far greater number of measurements and observations are necessary in order

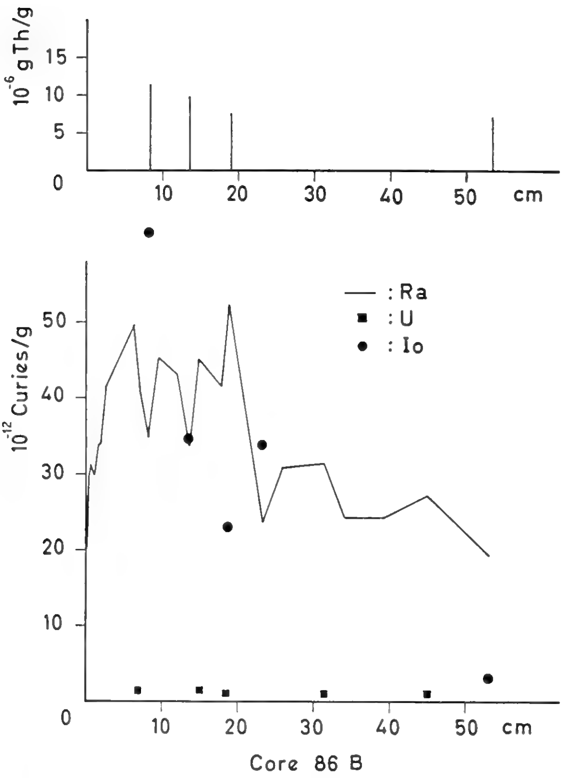


Fig. 6. Measurement on radioactive nuclides from Pacific clay core 86 B of the Swedish deep-sea expedition, 1947–1948. Graph shows activities of the following nuclides plotted against depth in core: radium (Kröll, 1955); uranium (Hahofer and Hecht, 1954); ionium (Picciotto and Poulaert, unpublished). At top is shown the thorium content of selected layers in the core (Picciotto and Wilgain, 1954).

to construct a complete picture of the radioactivity of the pelagic sediments. Meanwhile, the results of the aforementioned series of research may be summed up as follows (Table II):

1. The uranium content (1 to 4 parts per million) and the thorium content (5 to 15 ppm) of pelagic clays are similar to those of granitic rocks, and moreover, remain relatively constant.

2. In the younger upper layers, ionium is present in definite excess of its radioactive equilibrium concentration with uranium. This excess becomes markedly greater in cases where the rate of sedimentation is lower. In the Atlantic, where the rate of accumu-

lation of the clays is of the order of 1 cm per 1000 years the ratio of activities of ionium to uranium lies between 10 to 20. In the Central Pacific, where the rate of accumulation is of the order of 1 mm per 1000 years, this ratio is greater than 50. According to some as yet unpublished observations (Picciotto, Rosholt, and others) Protoactinium is also present in excess with respect to U^{235}, in the upper sediment layers.

3. The radium produced in the sediment, by ionium, has been clearly shown to migrate, in certain cases. Nevertheless, this diffusion of radium does not explain all the irregularities in its distribution. Figure 5 shows a case in which a secondary maximum concentration of radium is supported by a real maximum ionium concentration.

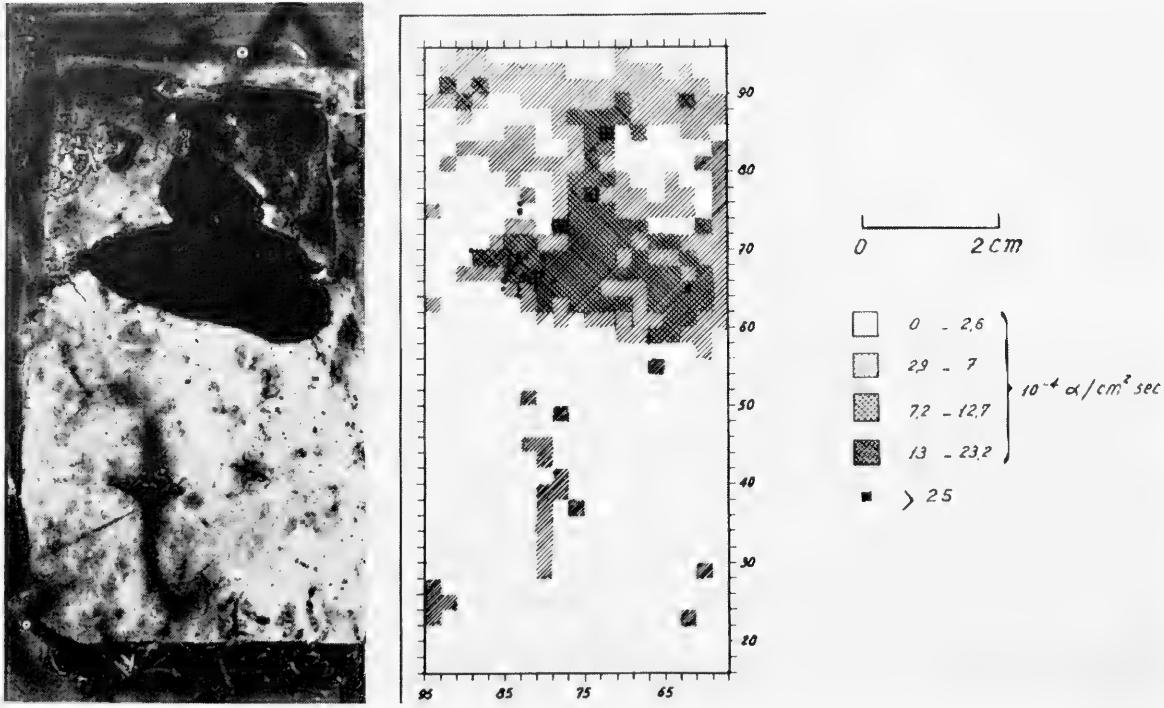
4. The ionium concentration generally decreases with the depth of the sediment, but this decrease is often found to be quite irregular, and does not appear to correspond to any simple model for the ionium distribution.

5. The mechanisms of transport of ionium from the ocean to the sediments are practically unknown. Recent observations obtained mainly from radioautographs of α particles (see Figs. 7–9) indicate that these mechanisms are varied and complex. These observations, moreover, stress the importance of certain authigenic minerals, for example phillipsite (Arrhenius and Goldberg, 1955), and the importance of biogenic constituents (Arrhenius *et al.*, 1957), much as in all marine geochemical problems.

6. The presence of beryllium-10 in Pacific clays has been shown by Peter's group (Goel *et al.*, 1957) and by Arnold (1956).

TABLE II. Radioactive Nuclides in Pelagic Clays

	Concentration, g/g dried clay	Activity, dps/g
K	$2{\cdot}4 \times 10^{-2}$	1×10^{-1}
U	$1 \text{ to } 4 \times 10^{-6}$	$2 \text{ to } 12 \times 10^{-2}$
Th	$6 \text{ to } 15 \times 10^{-6}$	$2 \text{ to } 6 \times 10^{-2}$
Io	$5 \text{ to } 30 \times 10^{-10}$	$0{\cdot}3 \text{ to } 2$
Ra	$20 \text{ to } 50 \times 10^{-12}$	$0{\cdot}3 \text{ to } 2$
Pa	$1 \text{ to } 6 \times 10^{-11}$	$1 \text{ to } 8 \times 10^{-2}$
Be^{10}	10^{-13}	10^{-4}



(a) (b)

Fig. 7. Distribution of α activity in pelagic sediments (Picciotto and Arrhenius, unpublished). (*a*) Photograph of vertical section of upper 8 cm of an equatorial Pacific core. (*b*) α activity distribution obtained from radioautographs. Sediment consists of Tertiary calcareous ooze with low activity, overlaid by thin layer of Recent clay with high activity. Active clay is seen to fill a large pocket near the surface as well as vertical channel lower down; both these features are caused by action of bottom-living organisms. This example demonstrates the large disturbances of the original layer distributions caused by such organisms. Note presence of highly radioactive centers scattered through the clay (see Fig. 8).

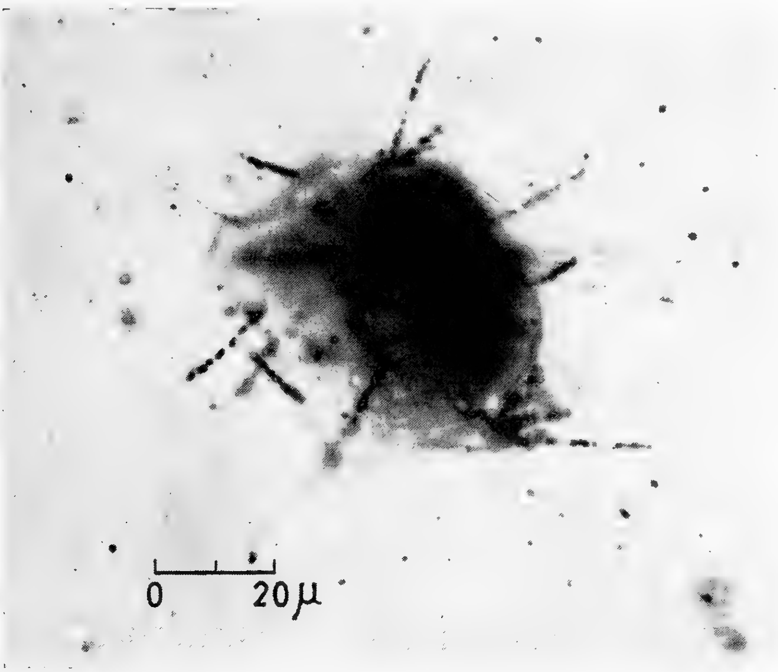


Fig. 8. Photomicrograph of pelagic clay particles embedded in a nuclear photographic emulsion. A highly radioactive debris of a fish skeleton emitting a number of α-particle tracks (Picciotto and Arrhenius, unpublished).

Finally, a number of communications submitted to this Congress hold promise of noticeably enriching our knowledge in these fields.

Possible Chronological Methods

Every radioactive nuclide present in the sediments may, in principle, serve as the basis for a particular method of age determination. We have, however, seen that the sole knowledge of the concentration of a radionuclide in a sediment does not suffice, and further information is, in fact, necessary. In the case of deep-sea sediments, this supplementary information is practically missing, and is generally replaced by more or less plausible hypotheses. Each of these hypotheses in combination with the use of a particular radionuclide constitutes a so-called method.

A brief review of the various methods in use, or suggested, up to the present, are in order.

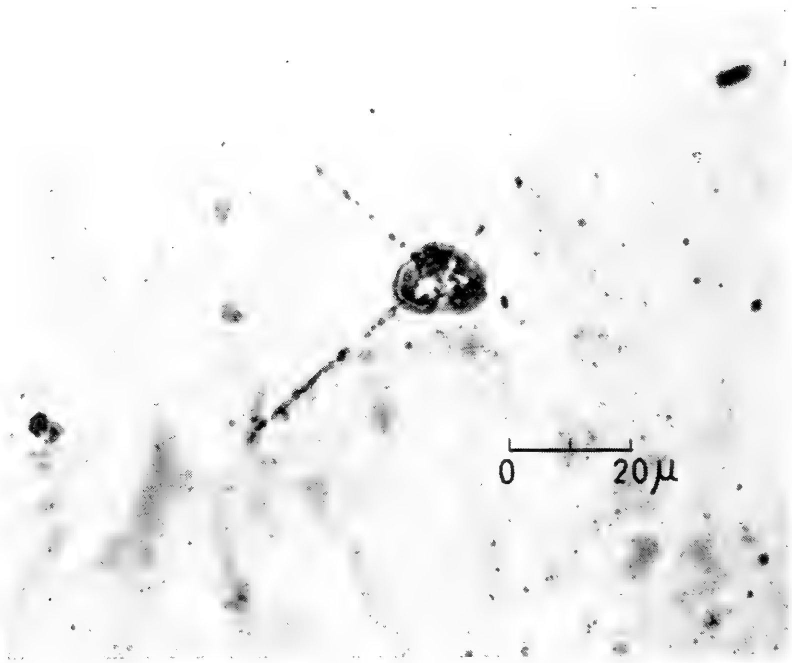


Fig. 9. Photomicrograph of pelagic clay particles embedded in a nuclear photographic emulsion. An active microcrystal of barite (?) (Picciotto and Arrhenius, unpublished).

Methods Based on the Decay of Cosmogenic Radionuclide

All these methods are based on the assumption that the flux of cosmic radiation remains constant with respect to time.

Carbon-14. The carbon-14 method is applicable to the carbonates of the calcareous shells of the planktonic organisms which constitute chalk oozes. Since the earliest observations carried out on Pacific chalk oozes by Arrhenius *et al.* (1951), a large number of important subsequent results have been published. This method is, at present, still the most reliable one, but unfortunately, is applicable only to intervals of time of the order of 25,000 years.

Beryllium-10. This element, for the moment, carries all our hopes for its use to date events between 500,000 and 10 million years. The development of this method is still rather unclear, but excellent reviews are to be found in the articles of Merrill *et al.* (1958) and of Peters (1957).

Methods Based on Decay of Ionium or of Protactinium

Ionium and protoactinium, separated from their long-lived parent elements in the sediment, should, in principle, be useful to measure intervals of time of the order of 300,000 and 150,000 years, respectively.

Ionium. The ionium method has become the most frequently used since the first radium measurements carried out by Piggot and Urry. Here again, a simple knowledge of the distribution of the element alone in the depths of the cores does not suffice, and two alternate hypotheses have been used in addition: (1) the initial concentration of ionium in the sediment is constant, at any given place (Piggot and Urry); (2) the initial concentration of ionium is not constant, but the amount of ionium precipitated in unit time, is constant, and, moreover, is independent of the rate of accumulation of the sediment (Pettersson). Each of these hypotheses finds an application in particular cases, but neither is of general value.

Protactinium. Any method of chronology based on the decay of this element will suffer the same restrictions as in the ionium method. Both these methods are based on the assumption that the concentration of the uranium in the ocean remains constant with respect to time.

Ionium-Thorium. This method, proposed by Picciotto and Wilgain (1954) and developed by Goldberg and Koide (1958), is based on the assumption that the nuclides ionium and thorium, being isotopes, are precipitated in the same ratio. In this case, the ratio of ionium to thorium in the sediment is a function only of age, and is independent both of the rate of sedimentation and of the rate of precipitation of the ionium. This basic assumption remains to be proved, as, even though they are isotopes, ionium and thorium may exist in different chemical forms in the ocean, and may not precipitate in a constant ratio. Furthermore, the method assumes that the ratio of uranium to thorium in the ocean has remained constant in time.

Protactinium-Ionium. This method (Sackett and Potratz, 1958; Rosholt, 1959) assumes that Io and Pa are precipitated in a constant ratio. This basic assumption appears to be quite plausible as Io and Pa, even though not isotopes, possess similar chemical properties. In this case, Pa/Io ratio in the sediment is only a function of the age (Fig. 10). The method presents a great advantage in that it would be independent of the concentration of uranium in the ocean with respect to time.

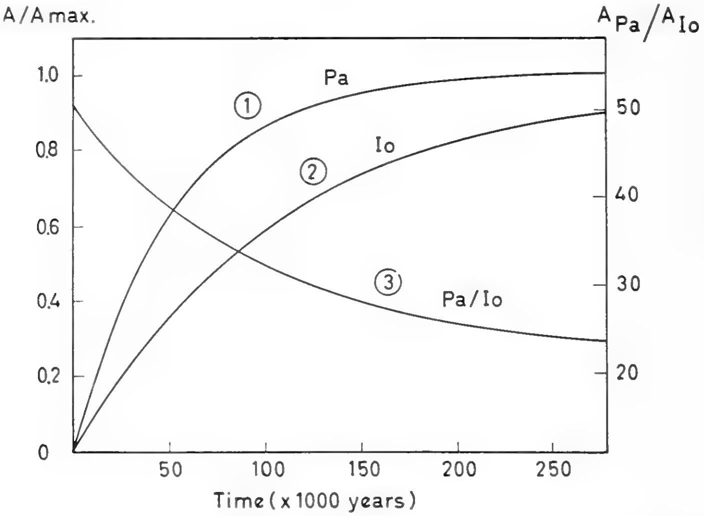


Fig. 10. Curves 1 and 2 show theoretical growth of protactinium and ionium from initially pure uranium. Curve 3 shows the change in ratio of activities of protactinium and ionium with time (Sackett and Potratz, 1958).

Methods Based on Growth of Ionium and of Protactinium

In the event of the uranium being separated from its daughter elements, the ratios of the activities of Io to U^{238} and of Pa to U^{235} would also make possible a measurement of age (Fig. 10).

This method would be applicable to aragonitic formations, which concentrate uranium at the moment of their formation, but which do not contain ionium. Barnes *et al.* (1956) applied the method to coral reefs. More recently, Tatsumoto and Goldberg (1959) showed its applicability to oolites.

Miscellaneous Methods

Finally, it would be useful to mention, among the methods under study, the argon/potassium and helium/uranium methods, applied to authigenic minerals and to fossils. Variations in the isotopic composition of lead also present interesting possibilities for study for the future (Chow and Patterson, 1959).

Conclusions

In concluding, a comparison should be made with the present state of development of the chronological methods employed in classical geology. Since 1945, the radioactive methods of geochronology have undergone spectacular development, especially in the field of pre-Cambrian geology. This successful period was, however, preceded by a static period of nondevelopment, lasting all of forty years. The sudden spurt appears to be due to two causes: (1) the development of new chemical and mass spectrometrical techniques, and (2) a clearer understanding of the fundamental geochemistry of the elements in question: uranium, lead, rubidium, strontium, etc.

In the chronology of recent sediments we are for the moment still in the static period. We find ourselves in need of more rapid and more precise methods for the analysis of ionium, protactinium, and thorium. We need a greater number of analyses of sediments and of sea water. But, above all else, we need a knowledge of the fundamental geochemistry of these nuclides. In what chemical form are they present in the ocean? What is the mechanism of their transport to the bottom? What happens to them, once precipitated on the bottom? The list of unanswered questions is too long to be given here.

I should like to conclude with a remark suggested also by comparison with work in classical geology. We find that a large number of the results of geochronological researches which were abandoned in the first instance because of the impossibility of interpretation, and which thus appeared to be meaningless, now, in the light of our present knowledge are of much interest. Their interest lies not in the ages which they indicate but in the information as to the mechanism of certain fundamental geological processes such as the formation of granites, metamorphosis, and orogenesis which may be deduced from them. It is equally certain that an important and often unexpected aspect of future research into the chronology of ocean sediments will lie in the information we shall thus gain—information on the fundamental mechanisms of the formation and the evolution of sediments in the ocean deeps obtained from results which today appear to be obscure or contradictory.

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Abyssal Benthic Organisms: Nature, Origin, Distribution, and Influence on Sedimentation

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THE term "abyssal" is used here in the same sense as in the *Treatise on Marine Ecology and Paleoecology* (Bruun, 1957); it thus includes the depths from about 2000 m to about 6000 m, or more than one-third of the surface of the globe. It does not, however, include those depths in more enclosed areas such as the North Polar Sea, the Mediterranean, the Japan Sea, or the Sulu Sea, where special conditions create temperatures different from those usual for the open ocean at these depths, namely about 1–4° C.

By far the greater part of the abyssal region is covered with a soft bottom, a fine ooze, or clay. Calcareous oozes, especially *Globigerina* oozes, dominate in depths of less than 4000 m, whereas abyssal clay is encountered only in depths exceeding 4000 m. In many places considerable debris of land plants is found (Bruun, 1959, Fig. 7), which seems to be important for the production of food with bacteria as the first link in the food chain.

Fauna

In general, the animal community of the abyssal zone may be called a soft bottom community. In any case, rock surfaces without any sediment covering exist only over a small fraction of the whole abyssal area. It is no wonder then that the abyssal fauna in many ways resembles soft bottom communities from shallower depths. The nature of such a community has been discussed by Ekman (1953), who also cites many examples of its representatives.

Among the dominant animals, only holothurians, especially of the order Elasipoda, like *Elpidia* and *Peniagone*, are mentioned here. Although other echinoderms among the ophiuroids play an important role, they often seem to have a patchy distribution. Asteroids are also fairly well represented, even by genera with a strongly calcareous skeleton like *Eremicaster* and *Dytaster*. Evidence of a curious way in which such animals may obtain part of their calcium supply is illustrated in Fig. 1.

As mentioned above, tree trunks, branches, and twigs, water-soaked coconut husks, bamboo stems, and a variety of other plant materials are of common occurrence in the deep sea, even astonishingly far from land. A thorough examination of the plant debris (Knudsen, 1960) revealed an extraordinary and specialized fauna primarily of boring animals, such as several species of the shipworm-like bivalve *Xylophaga*. Old tubes are sometimes occupied by small mytilids, amphipods, and worms of the genus *Nereis* (Kirkegaard, 1956, p. 68).

Quantitatively, the abyssal fauna is poor compared with those of shallower depths. The very few hitherto published data show, however, that locally a considerable abundance of animals may occur even at great depths (Spärck, 1956, p. 200; Zenkevich and Filatova, 1958, p. 156). During recent cruises of several Soviet research vessels a considerable number of quantitative samples have been obtained and summaries of some of the results have been published (Mokijevskij, 1953; Zenkevich and Filatova, 1958; Beljaev, 1953; Vinogradova, 1956, 1958).

Distribution

Not all the animals occurring there can be recognized as true abyssal forms, because they do not spend their whole life in this zone. Examples of this are species of deep-sea eels like *Synaphobranchus*, which in the early stages of their development lead an epipelagic life typical of Leptocephali larvae. Therefore, the pattern of distribution of such species is mainly influenced by suitable breeding places in tropical or subtropical waters. Another possi-

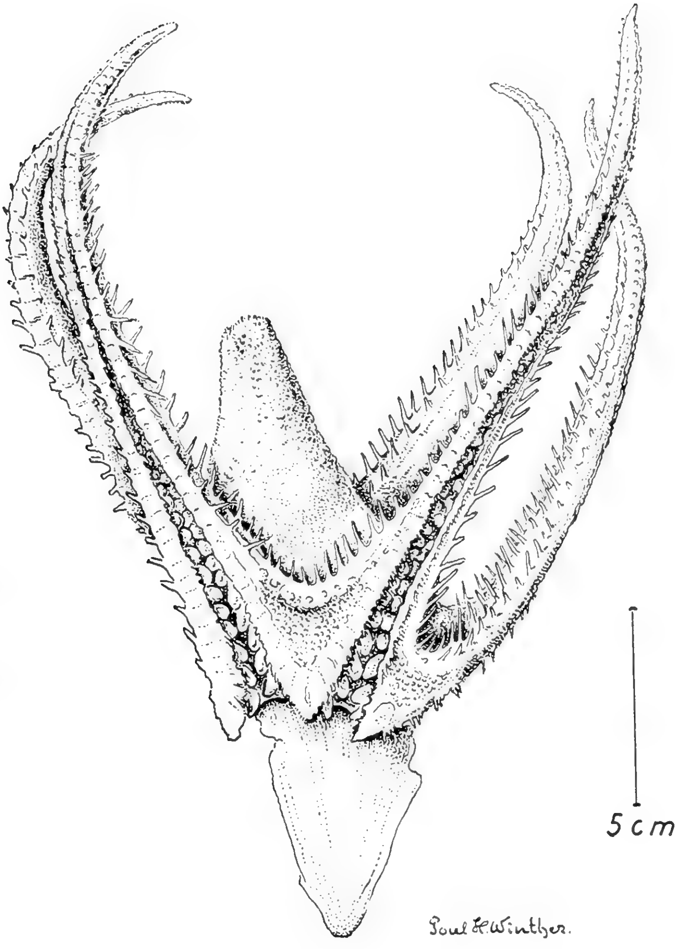

Fig. 1. A sea star, *Dytaster spinosus* Sladen, engulfing a fish bone covered with a little meat. The piece of bone inside the sea star is partly dissolved. (*Galathea* expedition, Station 235, Indian Ocean north of Madagascar, 4810-m depth. Drawn from a photograph taken on board and from the preserved specimen by Poul H. Winther.)

bility must also be considered, namely that deep-sea currents striking seamounts, or turbidity currents from continental slope areas, may carry many specimens into abyssal waters where the particular species may survive but not breed. A thorough study of the life history of selected animals on the slopes and neighboring abyssal regions within a restricted area is necessary to evaluate the significance of this.

Also for the true abyssal animals, meaning all species which live their entire life in the abyssal zone, much more collecting is needed before we can ascertain their distribution, etc. *Elpidia glacialis*, for instance, considered by Ekman (1953) to be restricted to the North Polar Basin, has now been found in all oceans (Zenkevich *et al.*, 1955; Hansen, 1956). Several more examples could be given. This does not exclude the possibility of certain species or higher taxons having a more restricted distribution, governed by the supply of food, the composition of the sediments, etc.

Origin

Without doubt the abyssal fauna stems from shallower depths. Even in the case of the recent Monoplacophora (Lemche, 1957; Clarke and Menzies, 1959), which hitherto have been found only in abyssal depths, it is still possible that other representatives of this order will be found on the slopes. A comparison of the abyssal fauna and the slope fauna indicates that the latter harbors a much more varied fauna than the abyssal zone. At the end of the last century, Perrier (1899) was aware that many ancient animal groups like the siliceous sponges and the eryoneid crustaceans were relicts of former shelf faunas. The find of the coelacanth fish *Latimeria* is a more recent example of this. The present abyssal group is on the whole of a fairly recent date. The hundreds of millions of years before the Pleistocene may very well have developed an abyssal fauna. However, the present fauna has only few species in common with this earlier one. The Pleistocene glaciation with the two polar ice caps must have produced a disastrous decrease in temperature in the abyssal zone, perhaps from about 10° to about 2° C, as indicated by Emiliani and Edwards (1953) so that only eurythermic animals could survive. A similar situation may have prevailed in the trenches and affected the composition of the hadal fauna; here only animals belonging to taxons higher than species may have survived from preglacial periods. The family of actinians, the Galatheanthemidae (Carlgren, 1956), which hitherto has been recorded only from trenches below some 6000 m, is an example of such survivors.

Influence on Sedimentation

Many years ago Darwin (1881) established the fact that burrowing land animals such as earthworms have an important effect in mixing the uppermost layers of the soil. A similar effect may be observed in any shallow water locality where *Arenicola*, for example, is abundant. In contrast to this only rather recently has the same phenomenon been taken into consideration in deep-sea sediments. Bramlette and Bradley (1942, p. 22) may be the first to note that "apparently mud-feeding animals have played a significant part in reworking the sediment, even on the floor of the abyssal parts of the ocean." In the last few years with the great improvement in deep-sea coring and photography, much evidence has accumulated for this sort of mixing. Among recent publications may be mentioned papers by Bernard (1958) and Pérèz (1958) with observations and photos from the French Bathyscaphe. They show small mounds up to 60 cm in height, together with holes and cavities of many various sizes on the bottom. These must be due to the activity of various larger bottom animals like crustaceans (*Ethusa*, *Galatheopsis*) and other animals known from deep-sea trawlings. From cores Picciotto and Arrhenius (unpublished) have found some beautiful examples of mixing down to at least 40 cm below the surface of the sediments. They suggest in one case that a worm channel has penetrated down to 26 cm; this might be one of the tubiculous polychaetes or one of the Pogonophora (cf. Arrhenius, Fig. 7, p. 142). Another example shows an organism which has dug a cavity into the bottom and this cavity has become filled with modern, highly radioactive sediment. Such a cavity could have been made by an irregular sea urchin like *Echinosigra* or some similar genus.

These examples tend to show that a better understanding of the upper layers of the deep-sea bottom will be achieved only when deep-sea photography or deep-sea coring is combined with a thorough collecting of the animals—by trawling or preferably by sampling the bottom with grabs.

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IV. Boundaries of the Sea

Coupling between Sea and Air

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PRACTICALLY all the physical, chemical and biological processes that take place in the sea are critically dependent on the fact that the sea has a free surface communicating with the atmosphere. The air-sea boundary phenomena and their relation to the interior processes in the sea have accordingly been subjected to an ever increasing interest by the oceanographer. In particular, a great deal of both theoretical and field work has been done on the mechanical-thermodynamic transfer processes at the sea surface. The importance of these processes in determining the physical state and the dynamics of the oceans is obvious. In fact, one can show, by the use of the basic laws of mechanics and thermodynamics, that for an ocean of given dimensions and of a given chemical composition the distribution of temperature and salinity as well as the motion of the water in the entire ocean is determined by a knowledge of the following boundary quantities: (*a*) the pressure and wind stress acting on the surface, (*b*) the net heat flux through the surface layer, (*c*) the net water flux through the surface layer (due to evaporation, precipitation, freezing, melting, and river supply).

In this case, we do not consider short-term fluctuations such as the astronomic tides, which require a determination of the body forces within the ocean, nor variations in the geologic time scale, which bring in different bottom processes, weathering effects, etc.

The fact that we can be satisfied in knowing the heat flux through the surface layer and do not need a determination of the interior heating function, is an essential simplification for comparisons with the atmosphere. This simplification, of course, results from the small amount of transparency in the sea which restricts all heat radiation effects to a surface layer a few meters thick.

When we can predict the interior state in terms of these forces, we shall have attained a real understanding of the physics of the ocean. Most of the earlier research in physical oceanography has been diagnostic, trying to relate different quantities such as the mass and velocity fields. These investigations are certainly most valuable and have supplied oceanography with many valuable theoretical tools, such as the "dynamic method" for computing ocean transports. They can, however, give us only part of the solution, which must come from models in which the boundary processes are the primary forces.

The first step is, of course, the study of the boundary processes themselves, and here much remains to be done. At present we try to construct a map of the yearly mean transport of water, of momentum, and of heat through the surface layer of the oceans. We cannot, considering all sources of error, give values correct within more than a factor of 2. Such uncertainty concerning the basic forces will prevent us from checking any theoretical model very exactly. How should we then be able to improve our present computations of these functions?

It seems that some new possibilities have now opened by the construction of reliable and accurate devices which directly measure the velocity and temperature fluctuations and their cross correlations in the sea. The possibility of making direct measurements of the turbulent momentum and heat transfer in the ocean surface layer by a hot-wire technique has been demonstrated by Dr. Kolesnikov at this Congress, and it should be possible to develop the method further. Direct measurements of the turbulent heat flux in the surface layer of the sea seem to be advantageous. In older computations based on measurements in the surface layer of the atmosphere, the total heat flux is given by a number of different processes: radiation, turbulent transfer, transfer of latent heat by evaporation and precipitation. It is difficult to estimate all these terms very accurately. If one measures in the sea a few meters below the surface, there is only one mechanism responsible for the heat transport, the turbulence, and the problem is considerably simplified. In the future one may hope to use automatic buoys that continuously register and transmit data on these transfer functions from different areas of the oceans. However, the measuring technique must first be developed further. Other problems, such as the influence of the buoy or of neighboring ships on the turbulent transfer, also must be studied with great care.

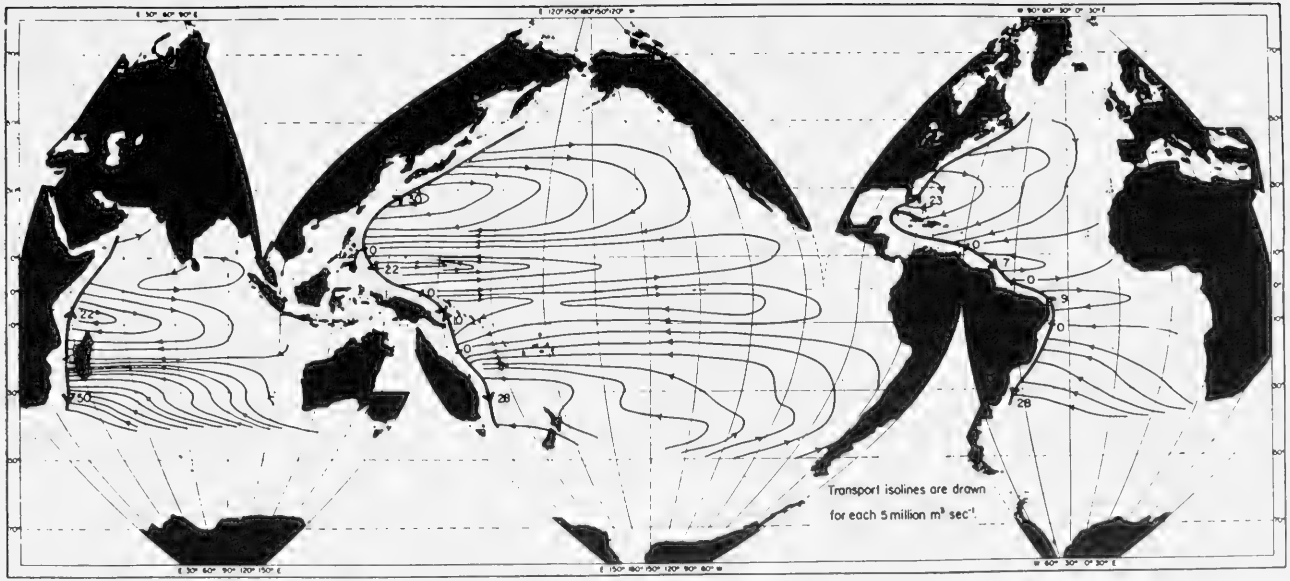
The second step in our attempt to formulate a more nearly complete model of the physical state and dynamics of the ocean is the setup of the appropriate model equations for the interior of the sea. The equations describing the transport of mass, salt, momentum, and heat within the sea are known, but we are in doubt about what values should be used for the turbulent exchange coefficients. These should be known provided the turbulence problem is solved. However, at present one should introduce measured values for these coefficients. Already by means of the present velocity data and the data for temperature and salinity in the oceans one can make reasonable estimates of both the horizontal and the vertical exchange coefficients. It must be admitted that this way of including the turbulent transfer mechanism is, from a theoretical point of view, unsatisfactory, but there is hardly any alternative.

The last step is to couple our interior model to the boundary processes mentioned and try to predict what the interior state and the dynamics of the oceans will be when we apply the measured forces at the sea surface. Here one runs into purely mathematical difficulties, arising from the complicated nonlinear form of the complete model equations. In principle, one could go directly to an electronic computer and try to solve the problem, but it may be better to approach the solution in steps, by a series of successively more complicated models that allow us to see the physical picture clearly at each stage.

In spite of all the theoretical difficulties, some advances have already been made on the problem. A model relating the vertically integrated ocean transport to the wind stress acting at the surface has been given by Sverdrup, and has been successful in predicting at least the major features of the ocean currents. The model is based on the assumptions that the friction, caused by vertical shear, and the Coriolis force together balance the pressure gradient, and that all motions disappear at great depths. The resulting equation predicts a northward transport proportional to the wind stress curl. Starting from a coastline where the normal transport is zero, one can from the continuity equation derive also the zonal transport all over the sea. The computation fails, however, when a second coastline is met, and the model obviously breaks down, at least locally. For theoretical reasons developed by several investigators, it seems obvious that the breakdown will take place at the western edges of the ocean basins. Accepting this idea, and placing boundary currents at these edges so as to fulfill all continuity requirements, one would find for the entire ocean system the circulation pattern given in Fig. 1. The wind stress data used are obtained from Hidaka and the Scripps Institution of Oceanography. The computation gives, of course, no information about the structure of the boundary currents. Detailed studies of conditions at the western edges have been made by Stommel, Munk, Charney, and others.

The map (Fig. 1) gives transport values that are of a correct order of magnitude, and the streamline pattern is in reasonable agreement with observations. Thus we may have some confidence in the simple Sverdrup model. Nevertheless, there is little hope that we could be satisfied with the Sverdrup model after we obtain sufficient, accurate data on wind stress and ocean transport to test the model critically. In fact, there are some obvious weaknesses of the Sverdrup model. To begin with, the model gives no information about how the water of the boundary currents separates at the western edges and then rejoins the Sverdrup circulation. At the southern tips of the continents the boundary currents are forced out into the sea, balancing the pure Sverdrup flow northward into the basin. This water must be taken care of by some mechanism other than the Sverdrup transport.

A second difficulty is the effect of convective sinking of water with winter cooling. This is a nonlinear process that may involve large quantities of water, say in the North Atlantic, and is not considered in the linear Sverdrup model. Other such nonlinear



Transport isolines are drawn for each 5 million m³ sec⁻¹.

Fig. 1. The Sverdrup transport and the boundary currents in the oceans corresponding to the annual mean wind stress field. The figures give the mass transport in million $m^3 sec^{-1}$. The wind stresses have been computed by Scripps Oceanographic Institution and by Hidaka.

processes of importance may be found along concentrated divergence or convergence bands in the oceans. In the model it is assumed that the convergence in the surface layer is a smooth function and is determined by the wind stress, but it is not impossible that real "cracks" also occur in the surface along which water sinks or rises. The computation of the vertical motion below the frictional layer from the geostrophic flow is also critical, and even small nonlinear terms may become important. These points may be of some general importance, since several later theories dealing both with the wind stress currents and the thermohaline circulation retain essential parts of the Sverdrup model.

If we consider the ocean as a system "forced" by the atmosphere, then one comes easily over to the problem of the atmospheric feedback. This is a most important one both for meteorologists and oceanographers, but it is also one of the most difficult to tackle. For a specific example of a feedback link, let us look at the wind stress transport problem. Assume that for some reason there is a small change in the wind stress acting on the sea. This will change the motion of the ocean current somewhat, and, hence, also the heat advected by it. Now, part of this heat is given to the atmosphere. If the heat transport in the sea is changed, the differential heating of the atmosphere is changed also. A change in this differential heating finally changes the winds and thus also the wind stress over the sea, whereby the circuit is closed. One may now ask whether or not an original perturbation running through the circuit is amplified or diminished. If it is amplified, we may eventually expect an instability that can result in oscillations, but if it is diminished, we may expect the system to return to its equilibrium. In the present case we can make a rough numerical estimate of the circuit. Consider, for example, the North Atlantic. The wind stress work over this basin is of the order of 10^8 kw. This figure gives the rate at which energy is given off to the currents by skin friction and the pressure thrust on waves. Of the heat advected by the currents an amount of the order 10^{12} kw becomes available to change the differential heating of the atmosphere. Since the temperature differences are small, the efficiency is low and, at most, a quantity of the order 1% of this effect can be used to increase the mechanical energy of the atmosphere. If more than 1% of this additional effect could be used to drive the ocean currents, we would give back to the ocean more than 10^8 kw, and instability may result. In the present case, however, no such amplifications are likely to occur, since certainly less than 1% of the total wind energy is used to drive the currents.

Also, if an amplification had occurred, oscillations would not necessarily be generated. Any original change in the wind stress would most likely give a reverse effect through the atmosphere. (An increase in the wind stress would, for example, increase the advection of warm water toward the poles and cold water toward the equator and so decrease the differential meridional heating of the atmosphere and the winds would slow down.)

Such a reverse feedback could cause oscillations, but only, as is shown by a closer theoretical analysis, when the characteristic response times of the atmosphere and the sea are comparable. In reality these response times differ greatly. The atmosphere will adjust to a change in the heating function within a few weeks, whereas the response in the ocean surface water, with a change in the wind stress, will take several years.

In the above example we see a feedback link that is most likely stable. The question arises whether there may be other dynamic-thermodynamic feedback couplings between the atmosphere and the ocean that may result in oscillatory states. The investigation of such a question is, of course, very difficult, since we do not have a real knowledge of all the complicated couplings that exist between the atmosphere and the ocean. One can, however, make some estimates based on our general experience with feedback systems. Such systems have, in fact, been studied a great deal in mechanical and electrical engineering.

A self-sustained oscillation in a feedback system requires, to begin with, that an energy flow take place through the system, to overcome the dissipation that otherwise will damp the oscillations. The atmosphere-ocean system certainly fulfills this requirement, the energy flow being sustained by the incoming solar radiation. A second requirement is, as said earlier, that the two processes in the atmosphere and the sea have comparable response times. It seems unlikely that the atmosphere itself will reveal any processes having response times of the order of a few years, as is required when considering couplings with the ocean surface water, or of several hundred years when considering couplings with the deep sea. One may attain sufficiently large time constants by including the ice in the polar regions. The essential coupling would then be between the ice and the sea, the atmosphere serving as the communicating energy link. It seems possible that the deep sea could be involved in oscillations caused by such a coupling. However, it must be emphasized that one cannot expect such oscillations to give rise to larger temperature fluctuations in the atmosphere, but rather that the fluctuations must be within the same range as those occurring in the deep sea. The reason for this is the enormous damping effect of the deep sea.

An intensive heating of the sea from the atmosphere, even over a period of a few hundred or a thousand years that corresponds to the circulation time of the deep sea, would produce only small changes in the mean temperature of the sea. The heat stored in the deep sea can be returned to the atmosphere at a later time, but the "quality" of this heat is then much lower, since it would be obtained under conditions with small temperature differences, and cannot be used so effectively.

For this and also for other reasons it is not very likely that the major climatic changes on the earth that have been recorded can be explained as a self-sustained oscillation. It should also be pointed out that the explanation of these changes based on a variable solar constant has very strong support from the recent detection of an increase in the solar constant by measurement of the light reflected from other planets.

Now, even though the feedback links between the atmosphere and the ocean do not produce any dramatic instabilities, they may be of importance. To make good long-range weather forecasts the thermal effects from the sea must be included, and the feedback effects will then also have to be considered. For this reason it is of interest to study further the characteristic responses of the sea to different mechanical and thermodynamic perturbations.

It would of course also be of the greatest value if one could make direct measurements of the feedback links in the atmosphere-ocean system. Under laboratory conditions experimental studies of feedback systems can be made by a frequency response technique. Certain periodic forces are applied, and the response characteristics of the system are studied as dependent on the frequency.

In nature one has few opportunities to arrange experiments of this kind. It seems, however, not impossible that even a feedback link such as the one seen in Fig. 2 may be subjected to direct experimental study. It was stated earlier that the effect needed to drive the ocean currents in the North Atlantic would be of the order 10^8 kw. If an additional effect of, say, 100.000 kw to 1 Mekw is applied, one would thus expect effects of the order of 0.1% to 1% in the circulation. Such effects normally drown in the general ocean "noise," but by keeping a fixed frequency for a sufficiently long time, it may be possible to separate out even such small signals. In this connection it may be of interest to mention that some studies are in progress as to the feasibility of attaining observable changes in the barotropic ocean circulation with a period of the order of a few days by bubbling air periodically through the water below swift surface currents, thereby changing the momentum exchange between the deep and the surface waters. Even small changes in the barotropic mode will be reflected in sea-level changes that can be measured by an appropriate pressure gage on the sea bottom. Whether or not any such experiments are

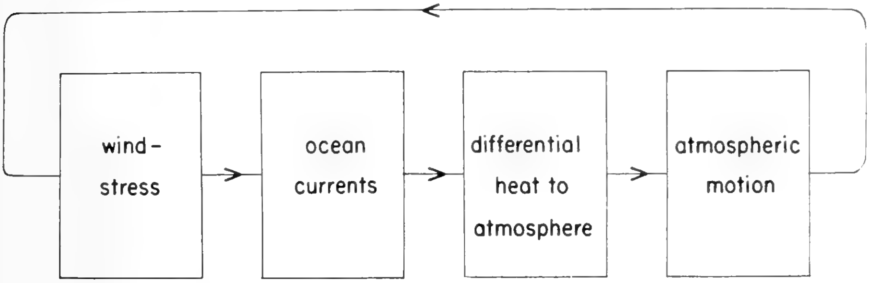


Fig. 2. Schematic representation of the feedback circuit relating the atmospheric circulation with the wind-driven ocean circulation.

ever developed, the discussion of them is stimulating because one comes to look on the ocean circulation from a new angle.

It seems likely that in the future we shall have reasons to discuss earnestly and perhaps also try several types of unconventional measurements and experiments that could supplement present oceanographic measurements and help to increase our understanding of the ocean and its coupling with the atmosphere.

The Exchange of Matter between Atmosphere and Sea

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THE rate of exchange of matter between atmosphere and sea has not been studied to any great extent in the past except for water vapor. For this the rate of evaporation from the ocean areas has been estimated by various methods, including the application of turbulent transfer theories. This transfer is relatively simple because mixing conditions at the sea surface can hardly limit the transfer. As to other compounds, the rate of exchange of oxygen has been studied by Redfield (1948), whose results indicate that conditions in the surface layer of the sea limit this rate of exchange. A similar state of affairs can be anticipated also for other gases in the atmosphere, including carbon dioxide.

A considerable amount of sea salt leaves the sea surface as particles at a considerable rate. Thanks to the remarkable work of A. H. Woodcock and his co-workers at the Woods Hole Oceanographic Institution, this exchange process can be reconstructed fairly well. The importance of this exchange for cloud formation and precipitation is already well known. Another aspect of this exchange, not often mentioned in the past, is the scavenging effect the sea salt particles must have on finely divided matter of foreign origin, for example radioactive debris, soot, and particulate matter from pollution sources.

With respect to the exchange of matter, one can obviously divide this into two groups: *gaseous* exchange and *aggregate* exchange, the latter pertaining to the mechanical ejection of sea water droplets at the sea surface and their removal by fallout and precipitation.

Transport Mechanisms at the Sea Surface

Matter is transported to and from the air-sea interface by two processes. One is statistical in its nature and is caused by random motion of molecules, as in molecular diffusion, or by random motion of parcels of air or water, as in turbulent diffusion. The other type is due to certain forces acting upon aggregates of molecules, as in the fall of particulate matter, or formation of strong jets of water from bursting bubbles.

In the vicinity of the air-sea interface one can formulate the vertical flux (i.e., flow rate) of any substance by

$$F = -K\frac{d\rho}{dz} + V\rho \tag{1}$$

where F is the flux per unit surface area, K a diffusion coefficient, molecular or turbulent, ρ the density of the substance, z the vertical coordinate, and V the vertical velocity of the substance due to gravity in the case of falling particulate matter or to the energy released in bursting bubbles in the case of jets of water.

The application of equation (1) in the immediate neighborhood of the air-sea interface requires some consideration. Under normal wind conditions, the turbulent region in the atmosphere is believed to terminate close to the interface where, at least in the air, a laminar boundary layer is generally supposed to exist. With current theories for computing it (e.g., Sverdrup, 1951), the thickness of this layer is of the order of 1 mm. Of course, nothing is known of conditions in the liquid phase, but it is not impossible that, on an average, such a laminar boundary layer exists there also. In this laminar boundary layer only molecular phenomena occur, so that the statistical part of the transport takes place only through molecular diffusion. For the transport of gaseous compounds, therefore, molecular diffusion is the only transport means close to the interface. As for aggregate constituents, i.e., particulate matter, molecular random motion of these will be extremely small, at least in the size range considered here. Hence, fall by gravity or rise by ejection from bursting bubbles are dominant in the transport of particulate matter close to the air-sea interface. Furthermore, it is rather unlikely that over the sea the impingement of particulate matter on the sea surface due to inertia forces can be of importance compared with the rate of fallout by gravity. Over vegetation-covered land areas impingement on leaves and other small obstacles seems to be a rather important process for removing particulate matter from an air stream.

Summarizing, we can state that the flux of gaseous matter close to the air-sea interface is given by

$$F_{\text{gas}} = -D\frac{d\rho}{dz} \qquad (2)$$

where D is the molecular diffusion coefficient. For an aggregate constituent, we consequently have

$$F_{\text{aggr.}} = V\rho \qquad (3)$$

in the same region.

For a gas the transport in the turbulent region, is, of course, by turbulent diffusion, but for particulate matter turbulent transport will take place only if the fall velocity of the particles in the laminar boundary layer is greater than in the turbulent region. It can be shown that even hygroscopic sea salt particles are transported downward almost entirely by gravity, as the moist laminar boundary layer hardly affects the average fall velocity of these particles.

In the case of simultaneous production of sea salt particles by bursting bubbles, the downward flux of particles in a steady state is balanced by an upward turbulent flux.

Aggregate Exchange

In viewing first aggregate exchange over ocean areas, the exchange of sea salts in particulate form is no doubt best known. It has been suggested, however, that organic matter enriched in surface films is also carried into the air by bursting bubbles. However likely this process seems, no direct evidence concerning it exists. We shall therefore limit our considerations on aggregate exchange to sea salt particles.

The rather extensive data furnished by Woodcock and his collaborators on the frequency distribution of sea salt particles in the air over oceans enables one to make certain estimates on the rate of fallout. Eriksson (1959b) has recently carried this out for three different regions by averaging available data. The results, shown as rate of fallout of mass per unit surface and logarithmic weight interval, are illustrated in Fig. 1 as a function of the weight of the

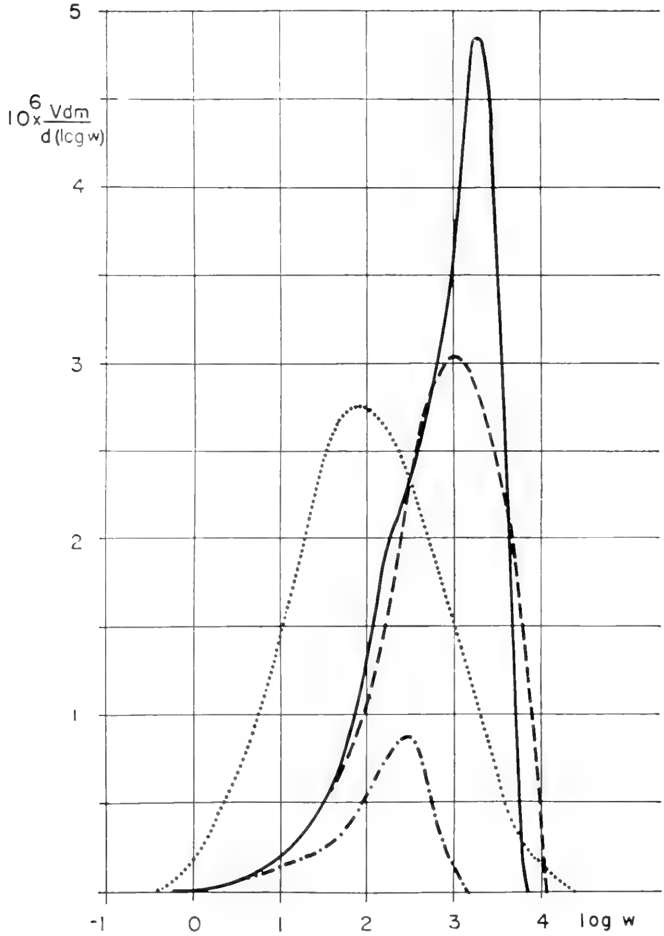

Fig. 1. Rate of fallout of sea salt particles and rate of production in bursting bubbles. The mass m in $\mu g \cdot cm^{-3}$, w in $\mu\mu g$ (10^{-12} g).

———	Hawaii
– – – –	Caribbean region
– · – · –	Pompano Beach, Florida
. . . . . .	Rate of production from bursting bubbles divided by 600

particles. The curves for the two oceanic regions of Hawaii and the Caribbean agree very well, whereas the curve for the Florida coast shows much less fallout. The total rate of fallout proportional to the surface area below the curves amounts to about 6×10^{-6} $\mu g\ cm^{-2} \cdot sec^{-1}$. From the total concentration of salt in the air, the average weighted fall velocity for the particulate matter is computed to be about $0.7\ cm \cdot sec^{-1}$. Considering that precipitation may remove as much as fallout, based upon arguments presented by Eriksson, the velocity of removal should equal about $1.5\ cm \cdot sec^{-1}$.

Blanchard and Woodcock (1956) made a very thorough study of the production of sea salt particles by bursting bubbles in breaking waves, and from their data Eriksson (1959b) also computed the rate of production in a breaking wave. These results also are presented in Fig. 1 by the dotted line on a 600 times smaller vertical scale as they give the same surface area as the Caribbean curve One interesting thing is that the maximum in the production curve is situated at much smaller particles than the fallout, suggesting a rather far-reaching coalescence process in the atmosphere that shifts the spectrum of the generated particles to the right. This is, in fact, in accordance with other observations, and suggests that these sea salt particles have a strong scavenging effect on foreign matter in the atmosphere.

As the rate of production per unit surface is about 300 times as large as the total rate of removal, one may infer that, provided breaking waves are the dominant source, about 0.3% of the ocean surface is always covered by foam patches from breaking waves. Observations by Munk (1946) on the frequency of foam patches and their size under different wind conditions give a coverage of 0.1 to 5% at wind forces of four or greater. An average of 0.3% for the whole surface area of the oceans is, therefore, not unreasonable.

Recently it has become fashionable to use the expression "residence time" for the ratio of mass to flux, an expression which is certainly of great didactic value. The average residence time for sea salts in the atmosphere is between one and two days. One must remember, however, that most of the flux is made up of particles greater than 10^{-3} μg, whereas a great deal of mass is found in particles less than this size. If transported inland, the residence time of successive fractions increases considerably after removal of the largest particles.

Gaseous Exchange

For particulate matter, it was found that the rate of exchange could be described by a transport velocity times the concentration of sea salt per unit volume. A likely figure for this transport velocity is 1.5 cm sec^{-1}. Only diffusion processes operate for gaseous matter, but despite this it may be of interest to see if gaseous exchange also can be formulated as transport velocity times the concentration. Dimensionally this can be inferred and can also be derived as follows.

For two substances *a* and *b* we can write the fluxes:

$$F_a = -K_a \frac{d\rho_a}{dz} \tag{4a}$$

$$F_b = -K_b \frac{d\rho_b}{dz} \tag{4b}$$

If it is assumed that the fluxes are constant and that $K_a = K_b$ in the whole region, we can write

$$F_a d\rho_b = F_b d\rho_a \tag{5}$$

and integrate between two levels z_1 and z_2. If the differences of ρ_a and ρ_b at these levels are designated $\Delta\rho_a$ and $\Delta\rho_b$, we have

$$F_a = \frac{F_b}{\Delta\rho_b} \cdot \Delta\rho_a \tag{6}$$

and writing $F_b/\Delta\rho_b = w$,

$$F_a = w\Delta\rho_a \tag{7}$$

i.e., the flux of the substance *a* is a product of a transport velocity w and a concentration difference $\Delta\rho_a$. This transport velocity is, of course, the same for all gaseous substances considered under the conditions given.

Consider now exchange between the air at a certain point and the sea surface, the exchange not being limited by conditions in the sea. We chose the lower level of integration to be at the air-sea interface where $\rho_a = 0$, i.e., we do not recognize molecules that are leaving the surface. Then we have the exchange rate

$$F_a = w\rho_a \tag{8}$$

between the sea surface and the level chosen.

However, we have ignored the effect of differences in the molecular diffusion coefficients in the laminar boundary layer. These differences are comparatively small, and it can be shown that, in the case of oxygen and in using water vapor evaporation for computing the transport velocity, the error introduced by the assumption $K_a = K_b$ is less than 10%.

Thus in the case of gaseous exchange we can also use a transport velocity as in the case of aggregate exchange discussed earlier. The concept of a vertical transport velocity for gaseous transports is not new, although it has been named differently in the past. It seems to have been used for the first time by Egnér (1932) in connection with a study of the loss of ammonia from manure spread out in a field. From the rate of evaporation of water and the relative humidity he estimated the volume of air per day and unit surface that had to get in close contact with the ground to account for the evaporation. He pointed out also that this volume corresponded to a *vertical wind.* This term is, of course, confusing. Recently Chamberlain and Chadwick (1953) studied the absorption of radioiodine from air by grassland and used the term "*deposition velocity*" for the rate at which radioiodine in air was absorbed by the ground. Bolin (1959), who discusses their results from various points of view, also uses this term, which is still not quite satisfactory. It really implies a unidirectional transport mechanism. A term like "transport velocity" is more adequate.

It may be of interest to discuss qualitatively the vertical variation of the transport velocity w when the sea surface is used as a lower reference level, because w defined in this way is in fact the velocity at which air from a certain level is brought in contact with the sea surface. In other words, w is the velocity of air exchange between a point in the atmosphere and the sea surface, but it must be remembered that this velocity of exchange pertains only to the sea surface, not to the sea or any larger portion of it.

Close to the sea surface w will be very high and take a value that corresponds to the rate of impact of molecules on the surface. As gradients near the surface are large, w will decrease rapidly as the distance from the surface increases, but farther away from the surface w will decrease more slowly because gradients are small; it always decreases with distance.

It was mentioned earlier that the rate of evaporation from ocean surfaces can hardly be limited by the mixing conditions near the sea surface. An estimate of w for the atmosphere at the height of a few meters can therefore be made from the rate of evaporation, the relative humidity, and the temperature of the sea surface. With Wüst's (1954) estimate of the rate of evaporation in trade wind regions (130 $\text{cm} \cdot \text{year}^{-1}$), a relative humidity from ships' measurements of 80% and a sea surface temperature of 25° C, the corresponding transport velocity would be 0.9 $\text{cm} \cdot \text{sec}^{-1}$. This should be the rate of air exchange between the sea surface and the observation level, say 8 m above the surface. If we used instead the average cloud base level where we know the water vapor density, we would arrive at a somewhat lower value for the transport velocity—probably 0.3 to 0.4 $\text{cm} \cdot \text{sec}^{-1}$. This would be due to a lower water vapor density at that level compared with the density at shipboard level. This value is of special interest as it can be applied to computations of the rate of tritium transfer to the sea by turbulent diffusion. The tritium concentration at cloud base level can be estimated from rain water analyses, and its concentration at the sea surface can be taken as zero. The turbulent flux is thus easily computed, and will be about twice the flux of tritium in precipitation.

With a still higher level, say the top of the troposphere, w with respect to the sea surface will probably drop to about 0.2 $\text{cm} \cdot \text{sec}^{-1}$ or less, as judged from the residence time estimated for various isotopes produced by cosmic rays near this level.

In returning to the transport velocity at shipboard level (0.9 $\text{cm} \cdot \text{sec}^{-1}$) it can be expected that this velocity also is going to transport the horizontal momentum of the air, ρu, to the sea surface, the horizontal motion of which is generally neglected. With 6 $\text{m} \cdot \text{sec}^{-1}$ for the average wind velocity at the same level, the momentum transport amounts to $0.9 \cdot 1.2 \times 10^{-3} \cdot 600$ g cm$^{-1} \cdot$ sec$^{-2} \cong 0.6$ dyne$\cdot$cm^{-2}. This produces the so-called wind stress on the surface.

We have found that the vertical transport velocity at the top of the troposphere is perhaps about 0.2 cm$\cdot$sec^{-1}. By converting this into residence time, this would be 40 days at most, but probably less on an average. Because w varies so strongly, the concept of residence time loses much of its significance. It can, however, be compared to the residence time of carbon dioxide estimated by Craig (1957). He found this exchange with the sea to be about 7 years or anywhere between 5 and 10 years. It is apparent from this that the carbon dioxide must be relatively well mixed in the troposphere. It is also apparent that some conditions in the sea must be limiting the rate of exchange of carbon dioxide with the sea. We shall examine several possibilities, but first a short description of the carbon dioxide system in the sea may be helpful.

The solubility of carbon dioxide in water is relatively high compared with that of other gases. One volume of water absorbs about one volume of carbon dioxide at equilibrium. Solubility depends on temperature, but this need not be considered in the present discussion. Part of the carbon dioxide reacts with water to form carbonic acid. The equilibrium, however, is such that dissolved carbon dioxide is the dominant molecular species. For all practical reasons, therefore, we can regard dissolved carbon dioxide as made up entirely of carbon dioxide molecules.

The rate of the hydration process forming carbonic acid is known to be comparatively slow, although no rate data exist. This process is, however, a very important step because carbonic acid dissociates to form bicarbonate and carbonate ions, which are dominant ionic species of carbon dioxide in sea water. The proportion of carbon dioxide to bicarbonate and carbonate ions in sea water is about 1 to 150. In the exchange of carbon dioxide with the sea it is apparent that the rate of hydration to carbonic acid may be of importance.

We may now investigate several possibilities to account for the observed residence time of carbon dioxide in the atmosphere. First we assume that the rate of mixing of the sea water near the surface does not limit the exchange of carbon dioxide into the upper layer of the oceans, the so-called mixed layer which contains as much total carbon dioxide as the atmosphere. Then the rate of hydration must be limiting and we can actually compute this rate. The rate of hydration can be expressed as $k \cdot m_{CO_2}$, where m_{CO_2} is the amount of free carbon dioxide in the mixed layer. This is about 1/150 of the atmospheric carbon dioxide. In order to keep pace with the rate of exchange with the atmosphere, k must be about 150/7 years^{-1}. This figure is far too small. Under laboratory conditions it would take at least a week to reach equilibrium in such a system, and this has certainly never been observed. Observations by Takahashi (1959) indicate that equilibrium for sea water is reached in about 20 min. We can then discard this possibility.

The other extreme assumption is that the rate of hydration is relatively rapid compared with the rate at which all carbon dioxide species molecular and ionic are mixed into the subsurface water. For this mixing we can use a vertical transport velocity analogous to that in the air. The apparent transport velocity of carbon dioxide in the atmosphere (using a residence time of 7 years) is equal to about 3×10^{-3} cm·sec^{-1}. As the volume concentration of total carbon dioxide in the sea is about 150 times greater than that in the air, the corresponding transport velocity from the sea surface into subsurface water should be $(3/150) \times 10^{-3} \sim 2 \times 10^{-5}$ cm·sec^{-1}. This figure seems extremely low. In fact, it is so low that, considering net evaporation of water, it would result in a salinity difference between the surface and subsurface of about 50%. The assumption of a relatively rapid hydration of carbon dioxide in the sea is therefore highly unlikely.

As a third hypothesis we assume that the rate of hydration is slow enough to prevent any appreciable exchange between different carbon dioxide species taking place while in contact with the atmosphere. This means that the transport velocity in the sea should be the same as the apparent transport velocity of carbon dioxide in the air, i.e., $\sim 3 \times 10^{-3}$ cm·sec^{-1}. This is because the volume concentration of free carbon dioxide in the sea and in the air is about the same. No serious objections can be raised against this value for the transport velocity in the sea, so we may accept it provisionally. Recently Kanwisher of the Woods Hole Oceanographic Institution (personal communication) performed a field experiment to study the rate at which excess carbon dioxide was given off from sea water. From his data the corresponding transport velocities were calculated as from 10^{-3} to 4×10^{-3} cm·sec^{-1}. These figures certainly agree well with those given above.

We may also compare the estimated transport velocity with the rate of exchange of oxygen studied by Redfield (1948) in the Gulf of Maine. He obtained different values for summer and winter, and if his values are converted into corresponding transport velocities, they become 3.6×10^{-3} cm·sec^{-1} in summer and 1.2×10^{-2} cm·sec^{-1} in winter. With a ratio of winter to summer areas of 1 to 2.5, the average transport velocity becomes 6×10^{-3} cm·sec^{-1}, which, if applied to the exchange of carbon dioxide in the atmosphere, will give a residence time of about 3.5 years. This time is in no way unreasonable. It therefore seems likely that in the exchange of carbon dioxide between atmosphere and sea the rate of hydration of carbon dioxide is slow enough to prevent any exchange between atmospheric carbon dioxide and bicarbonate and carbonate species at the surface. The exchange between the new carbon dioxide obtained from the atmosphere and the bicarbonate and carbonate takes place later when the original surface layer has been mixed into subsurface water.

It is interesting to note the much greater exchange rate in winter. For oxygen this is nearly four times as great as the summer rate. For carbon dioxide one might expect a still greater difference because of the greater variation of solubility of carbon dioxide with temperature. A great part of this difference between summer and winter is due to the turbulent mixing conditions and is reflected completely in the computed transport velocities. Redfield (1948) suggested that the larger winter values were primarily due to more frequent storms. It is also possible that the instability caused by cooling contributes substantially. This difference in transport velocities in the sea has also some bearing on the present carbon dioxide problem. Any model of the carbon dioxide exchange involving warm and cold surface waters of the sea must consider the greater rates of exchange anticipated in areas of cold surface waters. Eriksson (1959a) has recently computed the meridional transport of carbon dioxide in the air between warm and cold regions and estimated the pressure heads needed in sea water for this transport. Considering the more rapid mixing of cold surface waters the pressure head over polar waters should be divided by four. This will give an average of 0.2×10^{-4} atm instead of 0.8×10^{-4}.

If 5×10^{-3} cm·sec^{-1} is accepted as a rough value for the transport velocity between sea surface and subsurface water, this can be applied to some gaseous constituents which take part in the biological circulation in the sea. Sulfur in organic matter must be released as hydrogen sulfide. It is generally assumed that this hydrogen sulfide is oxidized in sea water to sulfate. However, hydrogen sulfide is a rather volatile gas, so escape to the atmosphere is quite likely to occur. Such an escape, if it took place, is of rather great geochemical significance. Assume now that none of the hydrogen sulfide is oxidized in sea water but is readily oxidized in the atmosphere, presumably to sulfur dioxide. With a transport velocity of 5×10^{-3} cm · sec^{-1} and a yearly rate of biological production of 75 μg·cm^{-2}, a figure computed from estimated rates of assimilation and the sulfur content in plankton, we ask what the steady state equilibrium in subsurface water is under such circumstances. The answer is 0.5 μg. liter^{-1}, a concentration so low that it cannot be detected by present analytical methods in oceanography.

Similar calculations can be made for nitrogen, if it is assumed that all nitrogen is released as ammonia in the biological cycle. With a yearly rate of production of 1800 μg·cm^{-2} and the transport velocity used above, the concentration in subsurface waters should be about 12μg·liter^{-1} or 12 mg·m^{-3}. Redfield and Keys (1938) analyzed waters from the Gulf of Maine and found values between 10 and 60 mg·m^{-3}. It is therefore quite possible that some of the ammonia released in the biological cycle in the sea goes into the atmosphere, especially in areas of high seasonal production. If this is applied to the North Sea area, it will perhaps account for some of the ammonia found in precipitation in western Europe. Over large areas of the sea this transport may be unimportant.

It is seen that the concept of a vertical transport velocity in the surface waters of the oceans is useful and simple to apply. Even if we know a likely average, it would also be most useful to know the geographical and seasonal variation of this velocity. From a purely physical point of view it should be possible to relate this velocity to wind stress and stability of surface water. Up to the present time no such relationships have been worked out, and even the primary data for such an evaluation are almost completely lacking.

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An Estuarine Model of the Sub-Arctic Pacific Ocean*

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Features of an Estuarine† System

THE basic requirement for the establishment of an estuarine system in any region is the presence of a supply of fresh water which exceeds the losses by evaporation or freezing.

Tully (1958) considered such conditions in coastal embayments (Fig. 1). He observed that the fresh water moved persistently outward from the embayment over the surface, entraining sea water from below to form a transition zone‡ in which there is a halocline. The upper part of the halocline is usually isohaline, because of mixing. It is called the upper zone, although it is considered to be part of the halocline. Both of these zones become progressively more saline along the path of outward flow, unless they are continually refreshed. Below the halocline is a lower zone in which the vertical and horizontal salinity gradients are small. Here, the motion is inward toward the source region.

Transport and Entrainment

From his studies Tully concluded that fresh water entering the surface accumulates locally over the denser (salt) sea water, until a surface pressure gradient is established sufficient to move the

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† The term "estuarine" is used in the same sense as Ketchum (1951) and Tully (1958) to refer to a region in which sea water is measurably diluted with fresh water.

‡ Tully (1949) introduced the term "zone" to designate a layer of consistent *structure* or properties in the sea. "Structure" denotes the disposition of sea water properties in a region, primarily in the vertical sense.

fresh water away from the source region at a rate equal to its supply.

The outward movement creates a velocity shear relative to the lower zone. This may be augmented by other shear stresses due to

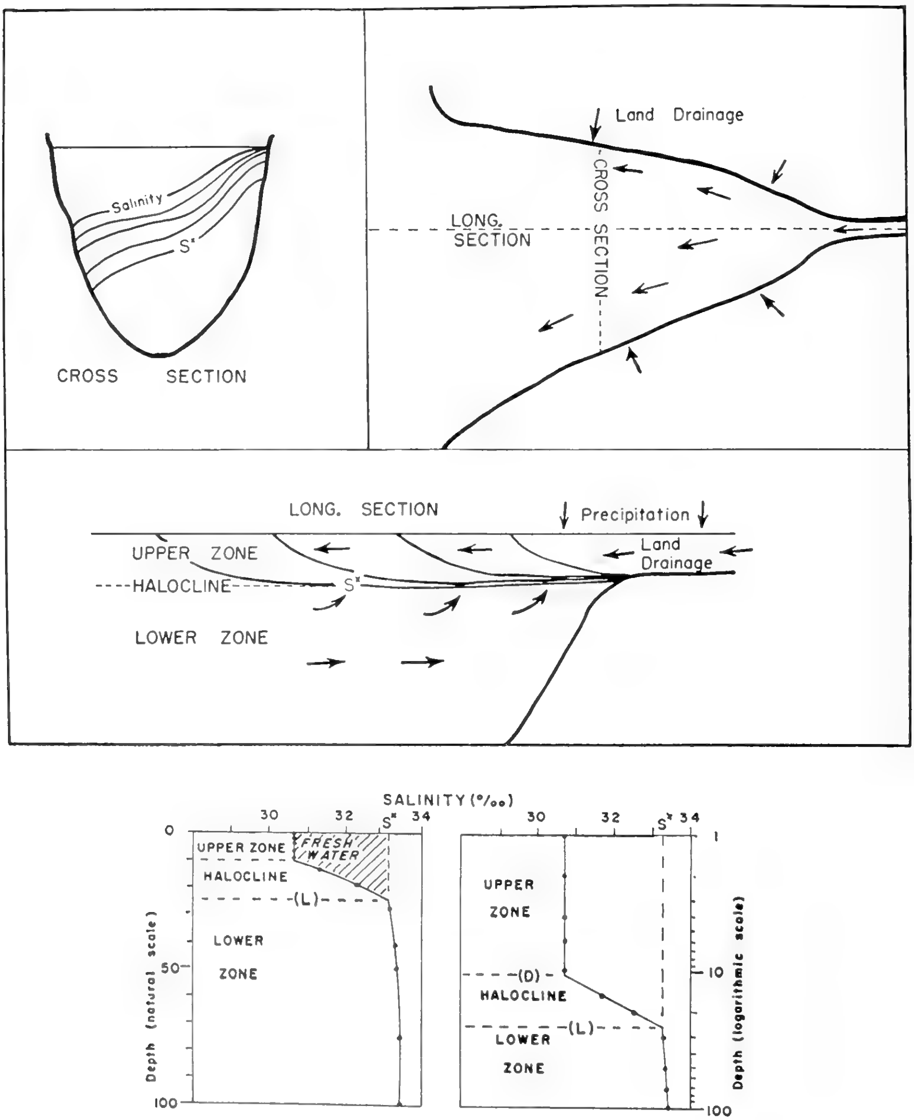


Fig. 1. Features of an estuarine embayment.

tides, winds, or current distribution. These shears provide the energy for mixing. Sea water mixed upward through the shear zone flows outward with the fresh water. Thus it is entrained and eventually lost from the region. It is replaced by an inward flow, toward the source region, below the shear zone. The density distribution in the transition (halocline) zone adjusts to provide the necessary inward pressure gradient force in the deeper water.

Fresh or mixed water transferred downward through the shear zone can never attain the salinity (density) of undiluted sea water in the lower zone. Hence there is a limit of downward transfer of fresh (mixed) water which must be near the lower limit of the shear zone. This is defined in the structure (Fig. 1) by the lower limit, L, of the halocline. In this position the mixed water must be transported toward the source region, and be preferentially available for upward mixing.

Thus the entrainment process may be regarded as a unidirectional upward transfer of sea water, coupled with a random mixing process in the halocline. The lower limit, L, of the halocline is the limit of the random mixing feature. At this limit the transfer of sea water is unidirectional upward.

The fresh water transport mechanism persists while there is a difference of salinity (density) between the zones. The entrainment process continually reduces this difference. It may be further reduced by loss of fresh water, by evaporation, or by freezing. When this difference vanishes, the structure is isohaline and the mechanism fails. However, if the upper zone is progressively refreshed, the halocline and the fresh water transport mechanism will persist.

Salinity Structure and Limits of Zones

From examination of extensive data, Tully (1957) concluded that the zone structure could be accurately delineated by plotting salinity as a function of the logarithm of depth. In this presentation, as illustrated in the last diagram of Fig. 1, the salinity distribution within each zone can be closely approximated by straight line segments. The intersections, D and L, of these segments define the limits of the zones.

Estuarine Features of the Sub-Arctic Pacific Ocean

It is possible to show that these features of estuarine structure occur in the sub-Arctic Pacific Ocean.

Salinity Structure

Figure 2 shows representative salinity structures at Ocean Weather Station "P." There is an *upper zone* of relatively isohaline, low salinity water, less than 33‰ extending to 85(±15) m depth.

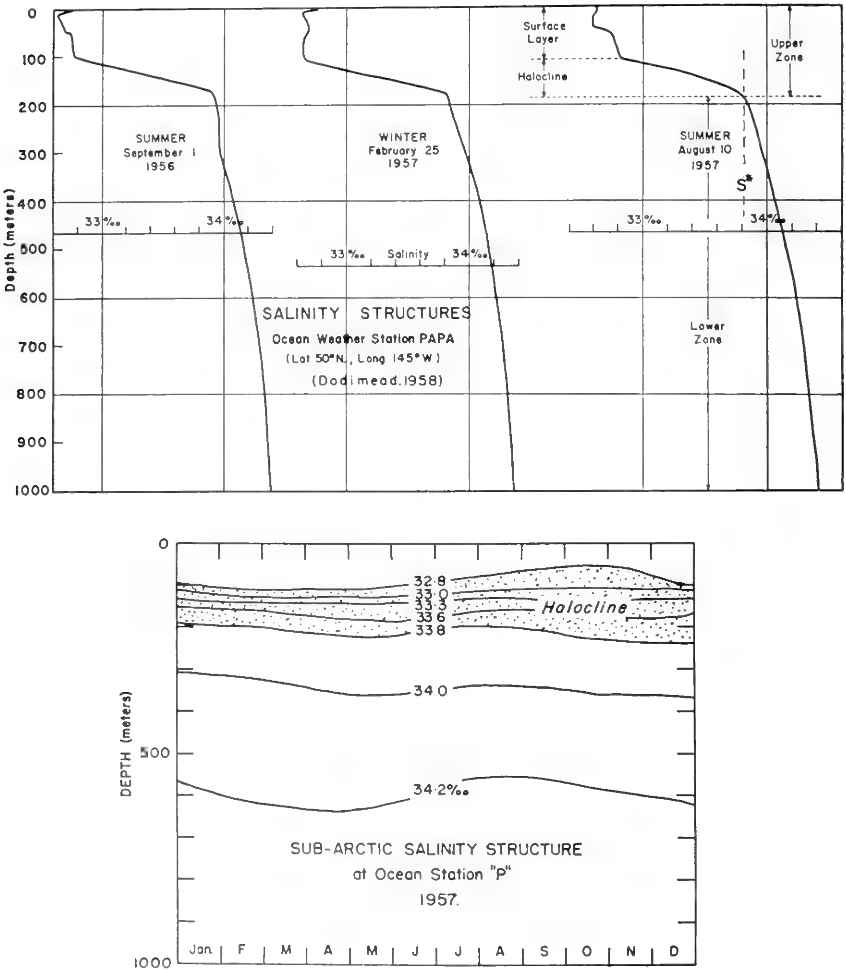


Fig. 2

Below this is a *halocline* extending to 200 (± 50) m depth in which the salinity increases to $33.8 \pm 0.1‰$ (the index salinity, S^*). Below this is the *lower zone* in which the salinity increases gradually with depth.

This structure has been observed winter and summer throughout most of the region northward of a sub-Arctic boundary located in the Polar Front. Dodimead (1958a) (Fig. 3) shows that southward of this boundary the salinity at the lower limit of the halocline became greater than 33.8‰, and a salinity minimum appeared below it. The halocline structure degrades and finally vanishes in a narrow band where the structure is nearly isohaline (Fig. 4). This also could be regarded as the southern limit of the sub-Arctic region (Tully and Dodimead, 1957). Pending further definition, these may be designated the inner boundary (Fig. 3) and the outer boundary (Fig. 4).

Within the sub-Arctic region, in the vicinity of the central Aleutian Islands, Dodimead (1958b) observed that the zone structure degraded to an almost uniform gradient, to about 400 m depth. This is attributed to extreme mixing in this locality.

Fresh Water

Jacobs (1951) (Fig. 5) showed that precipitation exceeds evaporation in the sub-Arctic Pacific Ocean and provides a continual, though irregular, source of fresh water in the region. The low salinity in the upper zone and the halocline structure there are consequences of this excess input of fresh water. The figure defines the source region.

Since the limit L of the halocline is the limit of downward transfer of fresh water, and can be identified in a logarithmic plot of the salinity structure, it is possible to compute the amount of fresh water above this limit. At any position this may be expressed as the fraction C of the depth L that would be occupied by the fresh water if it were segregated from water of index salinity S^*, at the limit L of the halocline (Fig. 1).

$$CL = S^*L - \frac{\int_0^L S dz}{S^*}$$

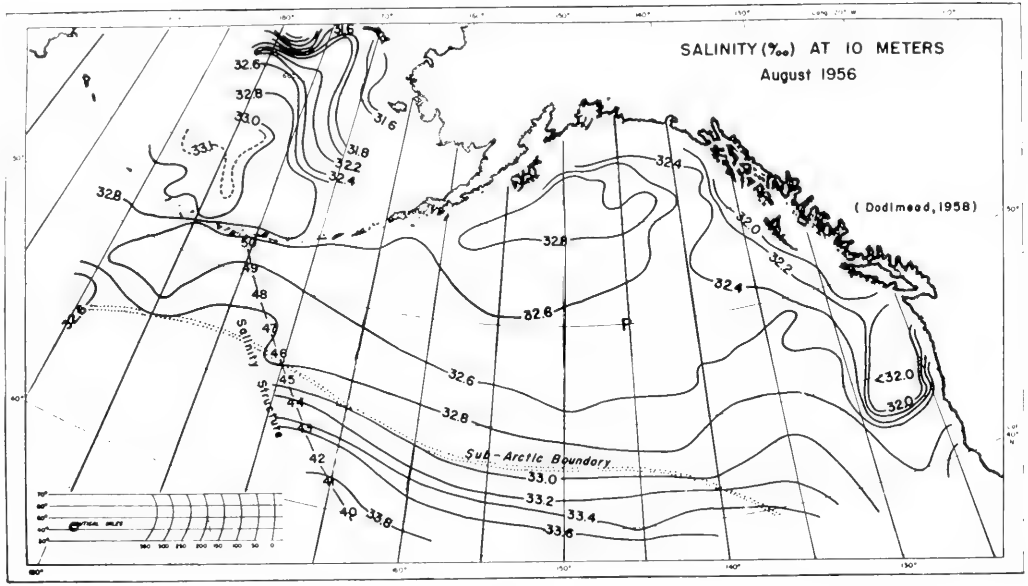


Fig. 3. *(Continued on facing page.)*

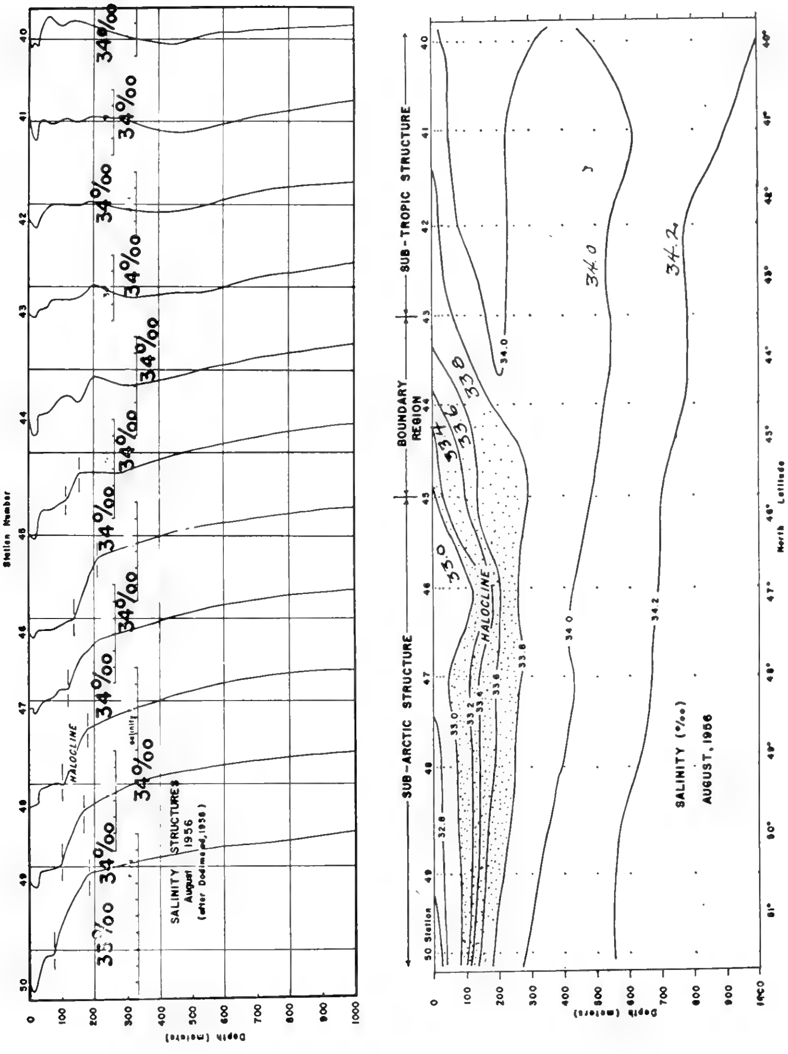

Station Number
40
41
42
43
44
45
46
47
48
49
50
Depth (meters)
0
100
200
300
400
500
600
700
800
900
1000
HALOCLINE
34‰
salinity
SALINITY STRUCTURES
August 1956
(after Dodimead, 1958)
SUB-TROPIC STRUCTURE
BOUNDARY REGION
SUB-ARCTIC STRUCTURE
50 Station
HALOCLINE
32.8
33.0
33.2
33.4
33.6
33.8
34.0
34.2
SALINITY (‰)
AUGUST, 1956
North Latitude
40°
41°
42°
43°
44°
45°
46°
47°
48°
49°
50°
51°

Fig. 3

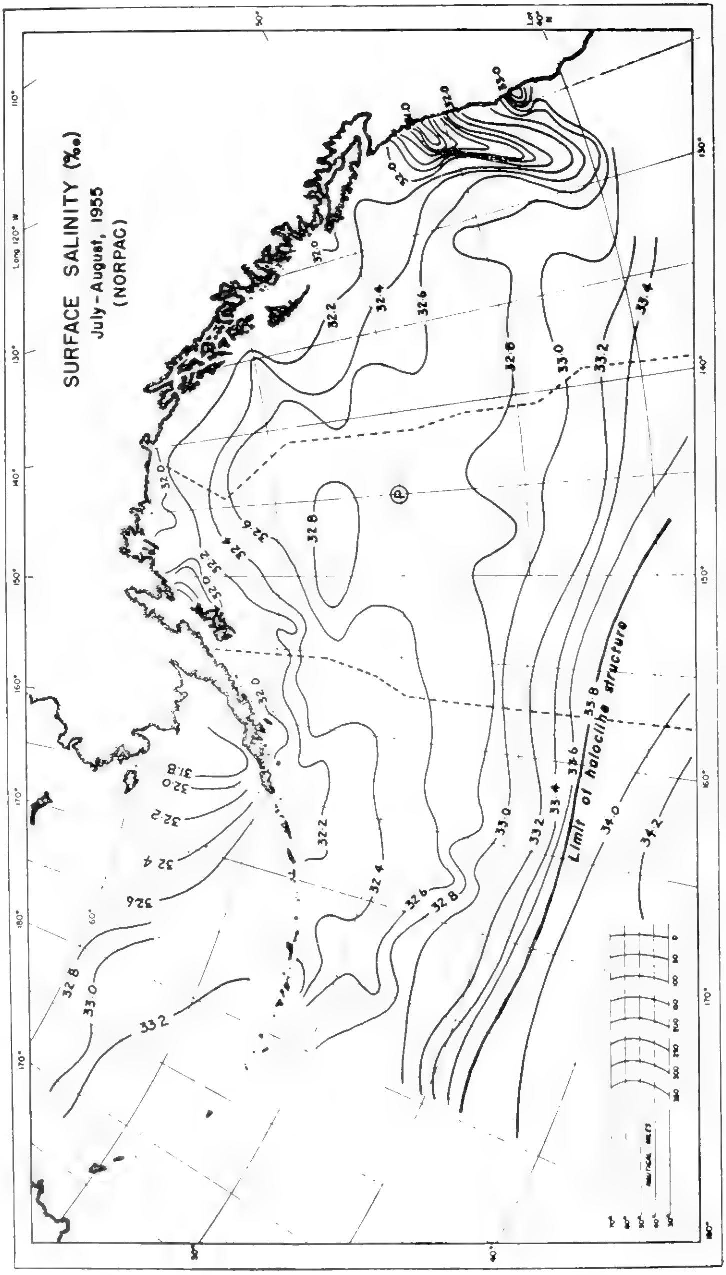
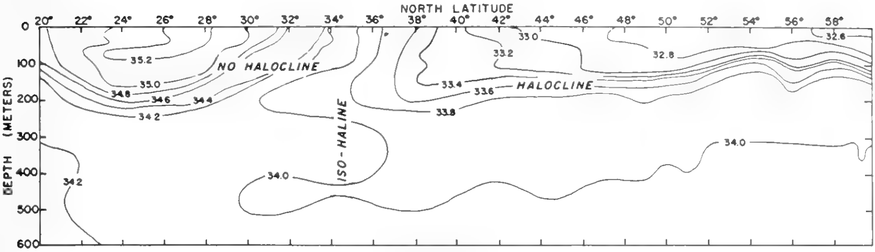
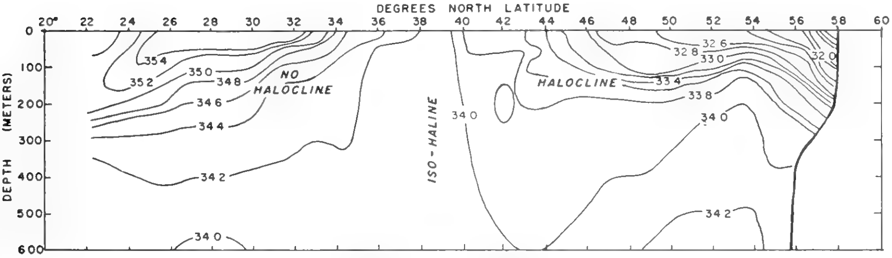


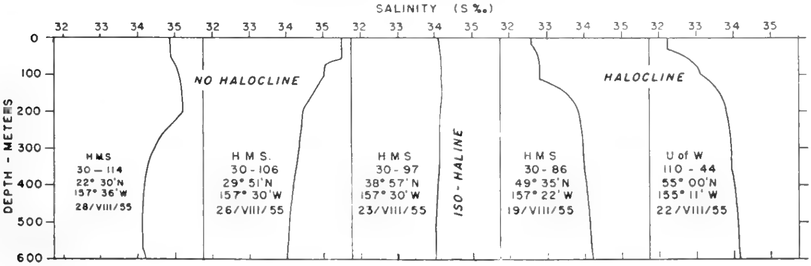
Fig. 4. (*Continued on facing page.*)



SALINITY (‰) STRUCTURE ALONG LONGITUDE 140° W.
August, 1955



SALINITY (S‰) STRUCTURE ALONG LONGITUDE 156° W (Approx)
July - August, 1955 (NORPAC)



SALINITY STRUCTURES ALONG LONGITUDE 157°W

Fig. 4

A representative distribution of fresh water in the eastern sub-Arctic Pacific is shown in Fig. 6. This varies from about 3 m in the vicinity of the salinity maximum in the Gulf of Alaska (Figs. 3 and 4) to about 5 m near the coast. Two features of this distribution are of interest. The average depth of fresh water is about 3.5 m, and the average rate of input is about 0.6 m per year (Fig. 5). Hence the average time of transit through the sub-Arctic region, as a whole (Fig. 4), must be about six years.

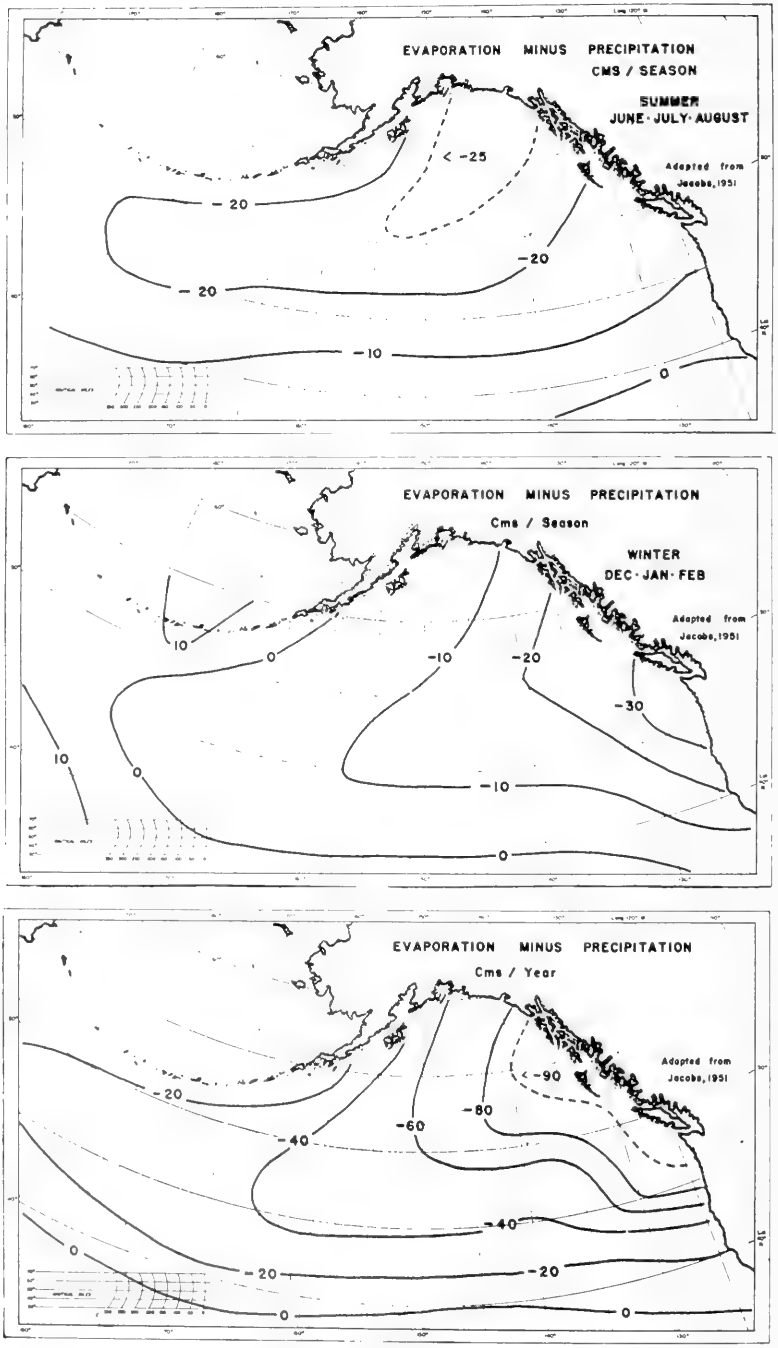

EVAPORATION MINUS PRECIPITATION
CMS / SEASON
SUMMER
JUNE · JULY · AUGUST
Adapted from Jacobs, 1951
< -25
-20
-20
-20
-10
0
EVAPORATION MINUS PRECIPITATION
Cms / Season
WINTER
DEC · JAN · FEB
Adapted from Jacobs, 1951
10
0
-10
-20
-30
10
0
-10
0
EVAPORATION MINUS PRECIPITATION
Cms / Year
Adapted from Jacobs, 1951
< -90
-80
-60
-20
-40
-40
0
-20
-20
0
0

Fig. 5

In the earlier study, Tully (1958) showed that the rate of upward transport, $-W$, of sea water through the lower limit, L, of the halocline was

$$-W = \frac{1 - C}{C} Q$$

where C is the fresh water fraction of the upper zone and halocline, $1 - C$ is the sea water fraction, and Q is the rate of input of fresh water. From Fig. 6, the fresh water fraction C is 2 to 5%, an average of about 3%. The rate of input is about 0.6 m per year over the area. Hence the average upward velocity must be about 20 ± 10 m per year over the area.

Circulation and Transport

Obviously there are other transport mechanisms operating to create the circulation in the sub-Arctic Pacific Ocean, for example, wind stress (Munk, 1950). In this region, from the confluence of the Kuroshio and Oyashio off the coast of Japan, the warm and cold waters move side by side toward America in the West Wind Drift. The surface gradient of temperature across the flow is called the Polar Front. Off the American coast the waters divide. Part turns south to form the California Current. The remainder turns northward and flows around the Gulf of Alaska. This water returns westward, close along the Aleutian Islands and is progressively dissipated into the Bering Sea. Most of this eventually joins the southward flow along Kamchatka. This is the origin of Oyashio and completes the circulation. Throughout the course of this flow an excess of fresh water is added to the surface and incorporated into the water masses. Hence this mixed water must eventually be transported to the sub-Tropics where the fresh water can be removed by evaporation, or to the Arctic Ocean.

Comparison of the limits of sub-Arctic structure (Figs. 3 and 4) with the circulation pattern (Fig. 7) shows that all the sub-Tropic water and part of the sub-Arctic water enter the California Current. A small part of the water in the Bering Sea is lost through Bering Strait to the Arctic Ocean (Saur *et al.*, 1954; Bloom, 1956). These define two regions of outflow of mixed fresh and sea water.

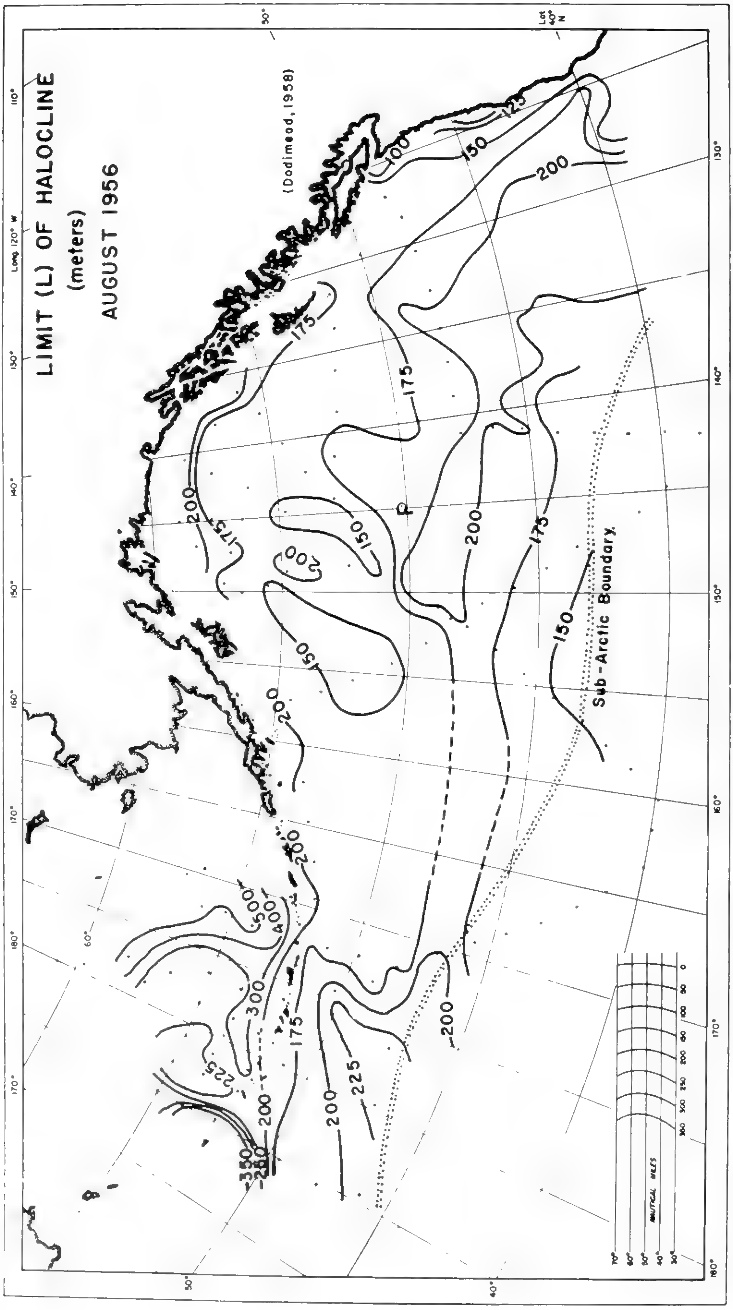


Fig. 6. (*Continued on facing page.*)

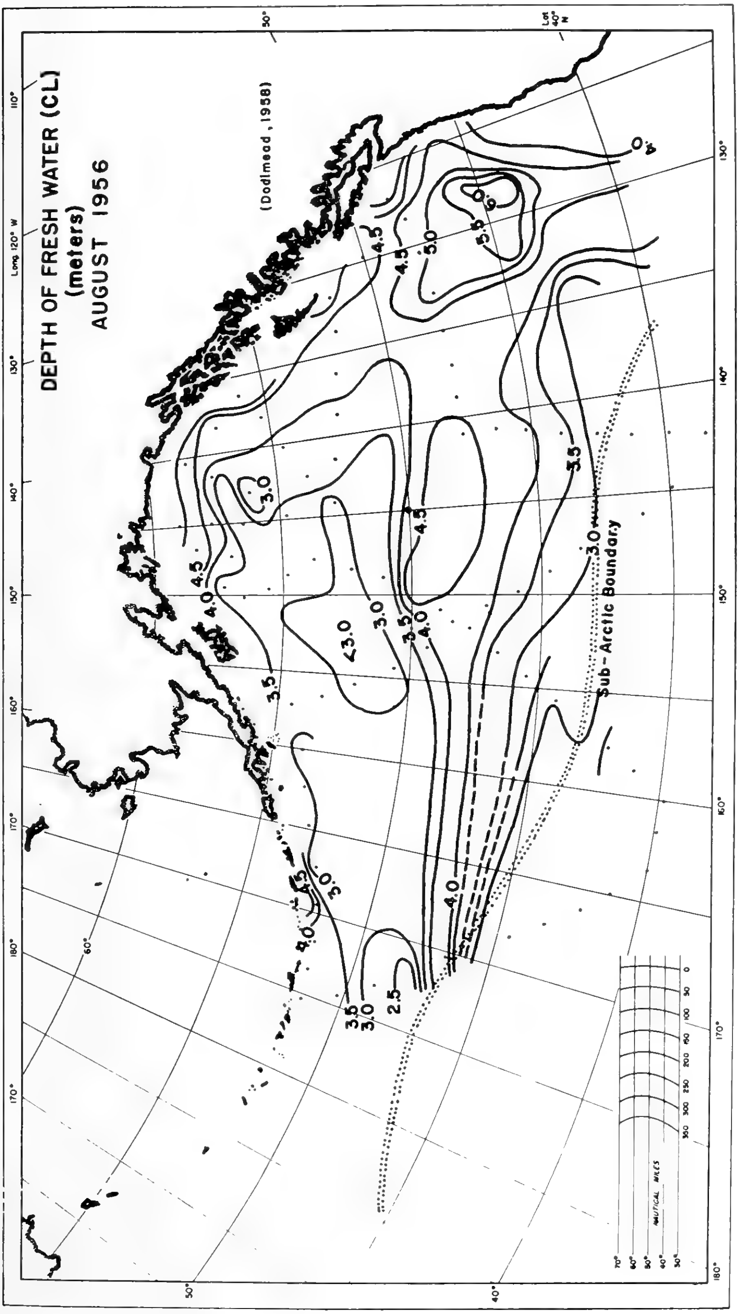

DEPTH OF FRESH WATER (CL)
(meters)
AUGUST 1956
(Dodimead, 1958)
Sub-Arctic Boundary
<3.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
NAUTICAL MILES

Fig. 6

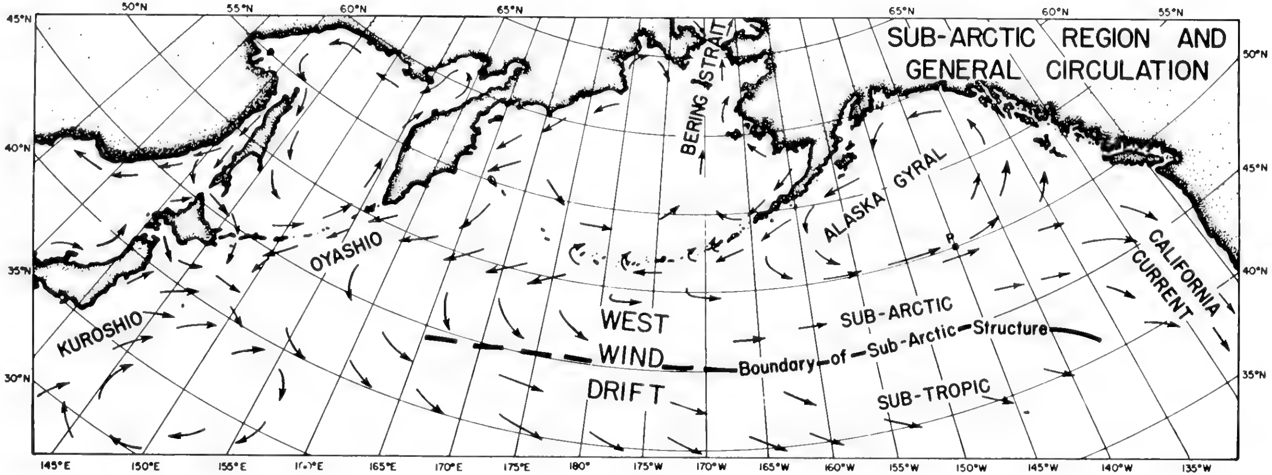


Fig. 7. *(Continued on facing page.)*

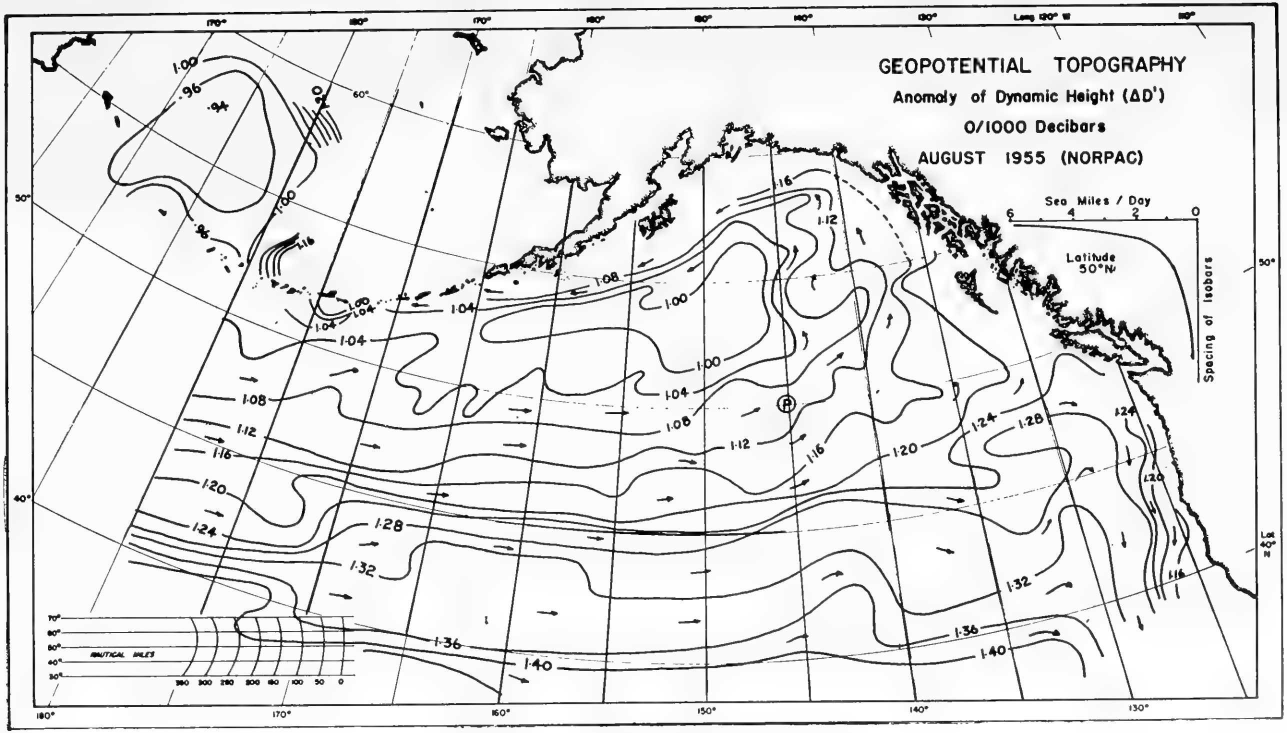


Fig. 7. *(Continued on following page.)*

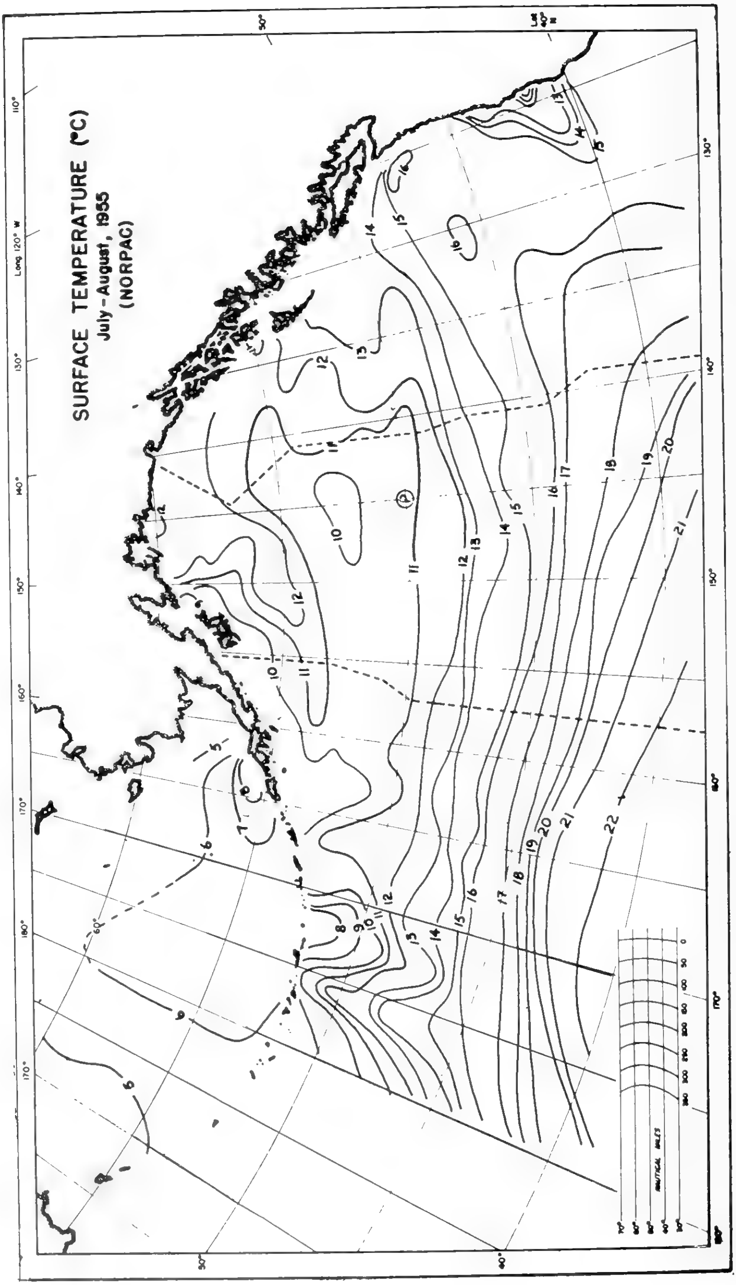

SURFACE TEMPERATURE (°C)
July-August, 1955
(NORPAC)
Long 120° W
110°
130°
140°
150°
160°
170°
180°
170°
50°
60°
40°
30°
130°
140°
150°
160°
170°
180°
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
NAUTICAL MILES
0
50
100
150
200
250
300
350

Fig. 7

The NORPAC (1955) data, recorded in the Oceanic Observations of the Pacific (Reid *et al.*, 1960), show that the halocline structure is continuous across the ocean north of the sub-Arctic boundary from Asia to America. Little is known of the lower zone circulation in mid-ocean; but, in the eastern Pacific, between Ocean Weather Station "P" and the Canadian coast, Bennett (1959) has shown a persistent intrusion of deep water. Thus at least one region of deep inflow is recognized.

Figure 6 shows that, in the eastern sub-Arctic, the amount of fresh water is greatest around the North American coast. From there the most direct route of transport, to the region of dissipation in the sub-Tropics, would be southward. However, because of the Alaska Gyral (Fig. 7) the direct southward route is denied to much of this water. Similar local centers of fresh water concentration occur in the Bering and Okhotsk Seas in gyrals contrary to the shortest routes of dissipation. Evidently fresh water transport mechanisms are present in the sub-Arctic Pacific Ocean. However, wind-driven and other mechanisms are also present, and determine the paths of flow within the region.

In the estuarine model previously described by Tully (1958) the requirements for net outward transport in the halocline, and net inward transport in the lower zone, and a shear zone in the halocline to provide energy for entrainment, were all accomplished by assuming opposite directions of flow in a narrow embayment, and a layer of no net transport in the halocline.

However, the required conditions are provided if the volume transport decreases along the path of transport in the lower zone, and increases along the path of transport in the upper zone and halocline, as sea water is entrained. Bennett (1959) showed that there were shear zones in the depths of the halocline (upper 200 m) over most of the Gulf of Alaska. Doe (1955) also observed this feature.

Conclusion

It is concluded that the features of an estuarine region, the salinity structure, the entrainment process, and the fresh water transport mechanism, are realized northward of a sub-Arctic boundary in the Pacific Ocean. Therefore, a comprehensive discussion of the oceanography of the region must include the estuarine model.

Some Features of the Model

Origin of the Lower Zone

The index salinity ($S^* = 33.8 \pm 0.1‰$) is remarkably constant northward of the inner boundary proposed by Dodimead (1958a) (Fig. 3). Further, the salinity gradient at the bottom of the halocline is small and less variable in time and space than the temperature gradient. These features were also noted in coastal estuaries (Tully, 1949; Waldichuk, 1957). Evidently the intruding lower zone is created by a mechanism which allows much less variation in the salinity than in the temperature.

It is suggested that the subhalocline waters in the eastern sub-Arctic Pacific Ocean may originate in the isohaline region at the outer limit of the sub-Arctic structure (Fig. 4). Northward intrusion, below the halocline, from the direction of this boundary has been observed by Bennett (1959) and Tully *et al.* (1959). The salinity characteristics of subhalocline water intruding from this source must be constant within small limits regardless of the depth of its origin (at least to 600 m). However, there is a temperature gradient in this boundary region; hence, the temperature of the intruding water depends on the depth of its origin.

Depth of Seasonal Effects

Precipitation and evaporation, heating and cooling, and wind mixing are all surface effects which vary with time. To the extent that these variations penetrate the halocline, they affect the constancy of the properties of the water there.

The depth D (Figs. 1 and 2) of the near isohaline upper zone coincides with the depth of the isopycnal layer in winter (Dodimead, 1958a). In summer, when the winds are light, some small haloclines appear in this upper zone, associated with the thermocline. They vanish in winter along with the thermocline, when all structure in the upper zone is destroyed by cooling and strong winter winds. This overturn determines the upper limit *D* of the halocline.

Earlier studies (Hollister, 1956; Tully and Dodimead, 1957; Tully *et al.*, 1959) have shown that there is a marked annual cycle of heating and cooling in the upper zone. The amplitude decreases with depth and becomes undetectable at about 120 m at Ocean Weather Station "P." This depth exceeds the depth *D* of wind mixing and includes the upper part of the halocline. In this zone, the seasonal heat exchange cannot be due to the overturn phenomena because of the presence of the salinity gradient in the halocline. Hence it must be dependent on the downward transfer feature of the entrainment process.

Since water from the upper zone is mixed downwards in decreasing proportions to the lower limit *L* of the halocline, it is evident that it must carry its temperature and all other properties with it to this limit. However, the water being transferred downward is being mixed with ever increasing proportions of water originating at the limit *L* so that the surface-induced temperature cycle is masked by variations in the entrained waters, and becomes unrecognizable in the halocline.

The variation of fresh water input with time is small. This is evidenced by the studies of Doe (1955) and Dodimead (1958a) which show that the surface salinity distribution (Figs. 3 and 4) is consistent from winter to summer within about 0.2‰. There is little or no seasonal variation of salinity at the limit *D* of the upper zone. Hence the salinity gradient in the halocline is not a seasonal function.

It is concluded that the lower limit *L* of the halocline is well below the limit of recognizable surface-induced seasonal variations in the sub-Arctic Pacific Ocean.

An Application of the Model

Identification of Halocline Water

It has been established that all the sea water in the halocline and upper zone of the sub-Arctic region enters these zones through the lower limit L of the halocline, and that the vertical transfer here is unidirectional upward. Since the salinity is nearly constant on this boundary, and it is well below the limit of recognizable seasonal variations, the intruding sea waters may be identified here by their temperature alone.

Once they are entrained, these primary sea waters are mixed, heated and cooled, and diluted with fresh water. Hence, as they approach the surface their identities become obscured. However, by recalling that the entrained sea water constitutes 95 to 98% of the halocline and upper zone, and that the rate of vertical transfer is of the order of 20 ± 10 m per year, it is evident that any change of the water on the interzone boundary presages corresponding changes in the shallower waters, despite surface effects.

This interzone boundary may be defined in the logarithmic plot of normal oceanographic data from serial observations. In this definition, based on structure, all the data in the halocline and lower zone are used. Minor variations in structure are smoothed. The conclusions are objective. It can be applied in any region where there is a halocline, whether or not the salinity at its lower limit L is constant, e.g., between the inner and outer sub-Arctic limits (Figs. 3 and 4).

Northward of inner sub-Arctic boundary (Fig. 3) this procedure may be *approximated* within small limits of error, by plotting the temperature corresponding to the index salinity, 33.8‰. This is permissible because of the constancy of the salinity at this lower limit L. The required temperature is readily determined from a temperature-salinity (T-S) diagram (Helland-Hansen, 1916). The typical relations in Figs. 8 and 9 show that the temperature gradient is small in the vicinity of this value. Hence the error associated with normal variation of the index salinity (±0.1‰) is negligible.

By using the *approximate* technique, the data from the series of quasi-synoptic surveys have been plotted as shown in Fig. 10. In these diagrams there are warm waters (warmer than 6.5°C) in the Polar Front and near the coast (shaded), separated from a cool water (cooler than 4°C) area in mid-ocean and the Gulf of Alaska.

These may be compared to the conventional T-S analysis made

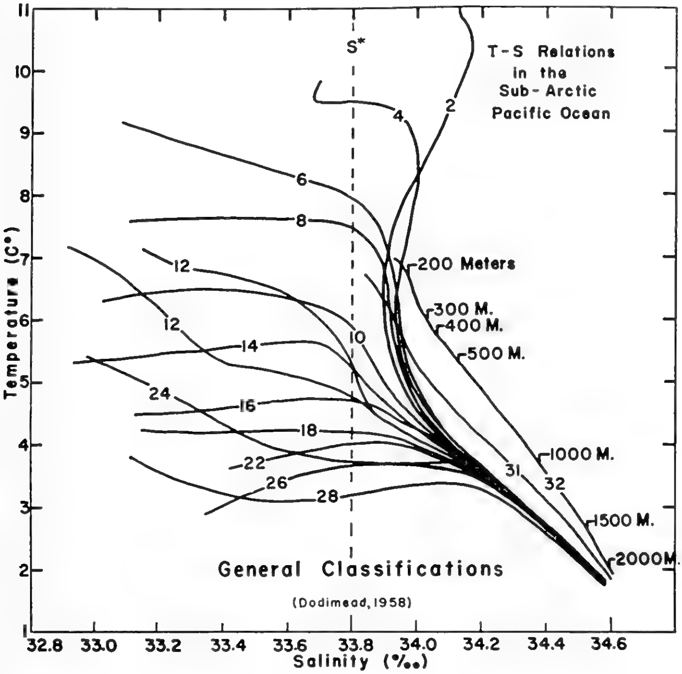
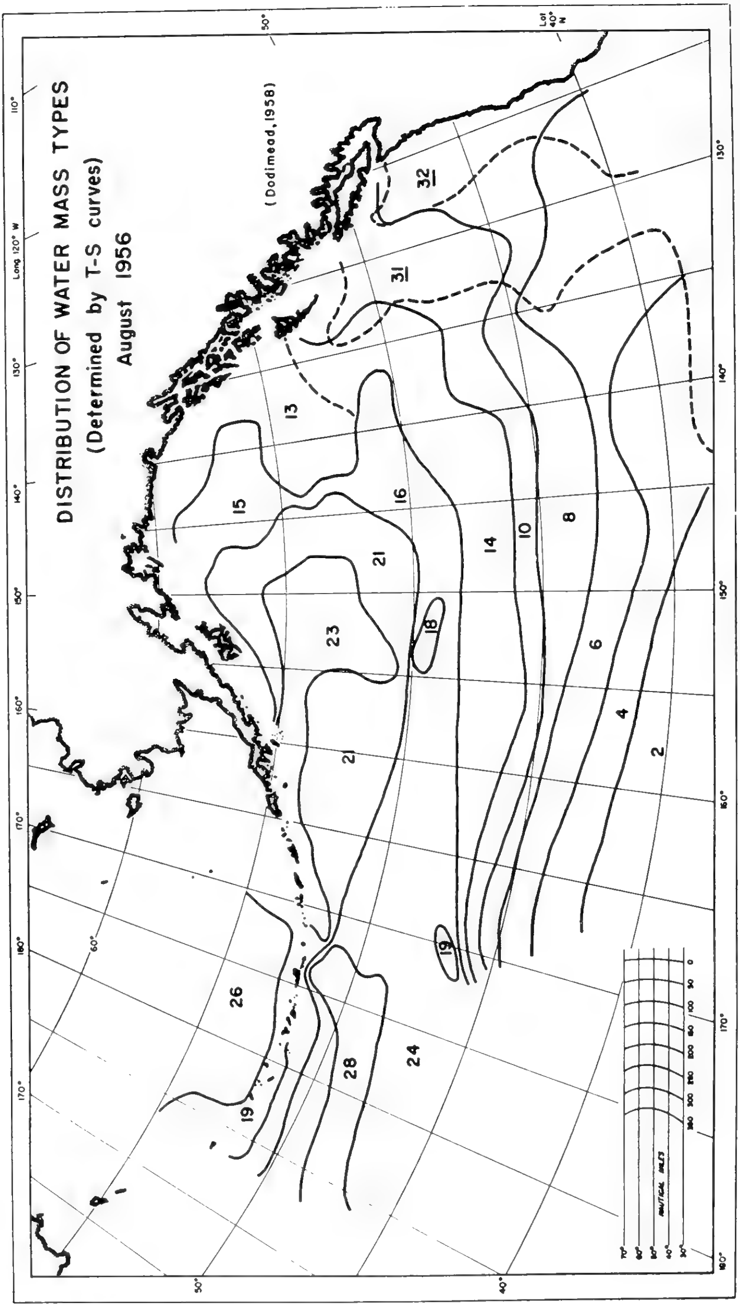


Fig. 8

by Dodimead (1958) as shown in Figs. 8 and 9. Here the water masses in the halocline were classified arbitrarily according to the temperature level in the halocline as shown in the first diagram, and their distribution in the region was deduced from the data as shown in the second diagram. By comparing this with the corresponding halocline (temperature on salinity 33.8‰) plot, for August 1956 in Fig. 10, it is evident that the interpretations coincide in every important respect. Perhaps for this purpose this halocline plot is preferable to the conventional *T-S* interpretation in Fig. 9 since it requires no arbitrary definitions, and provides single-valued numerical indices of the waters.

The sequence of diagrams in Fig. 10 shows a progressive northward intrusion of relatively warm water (shaded) past the Canadian coast through 1957 and 1958. These may be compared, regardless of season, because the data are everywhere below the level of seasonal influence.


DISTRIBUTION OF WATER MASS TYPES
(Determined by T-S curves)
August 1956
(Dodimead, 1958)
32
31
13
15
16
21
23
18
14
10
8
6
4
2
19
26
28
24
19
21
Long 120° W
110°
130°
140°
150°
160°
170°
180°
170°
Lat 40° N
50°
60°
50°
40°
NAUTICAL MILES
0
50
100
150
200
250
300
350

Fig, 9

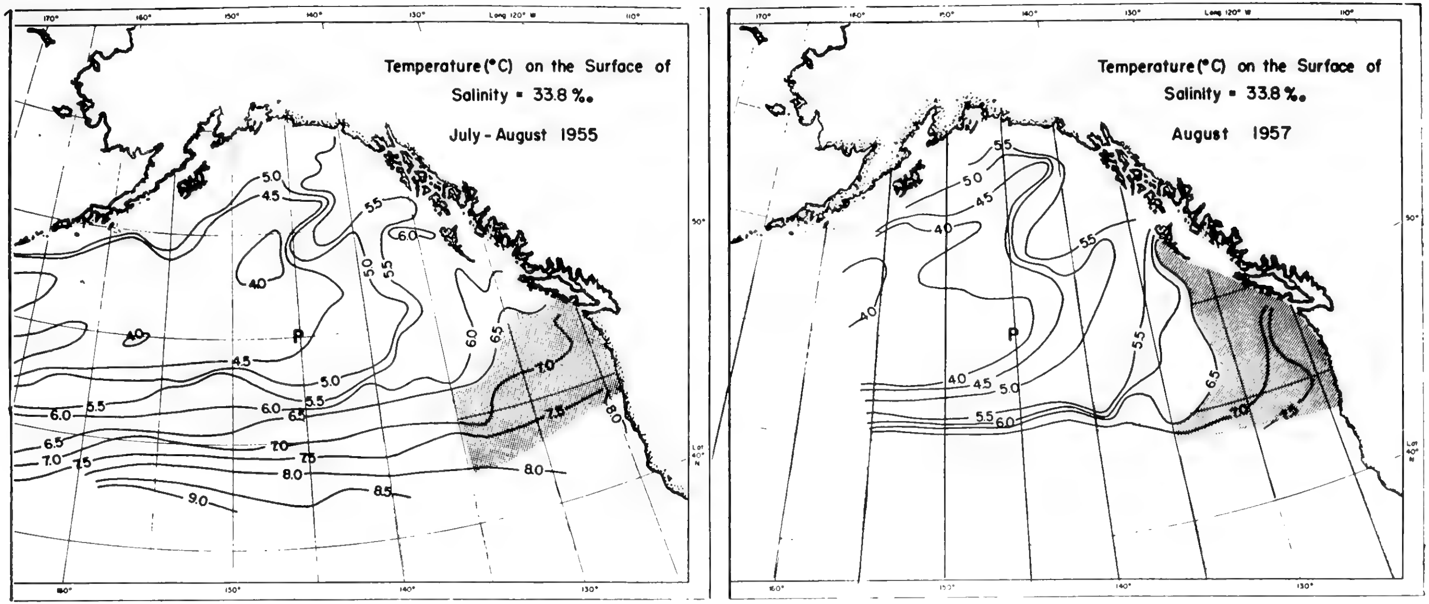


Fig. 10. (*Continued on following page.*)

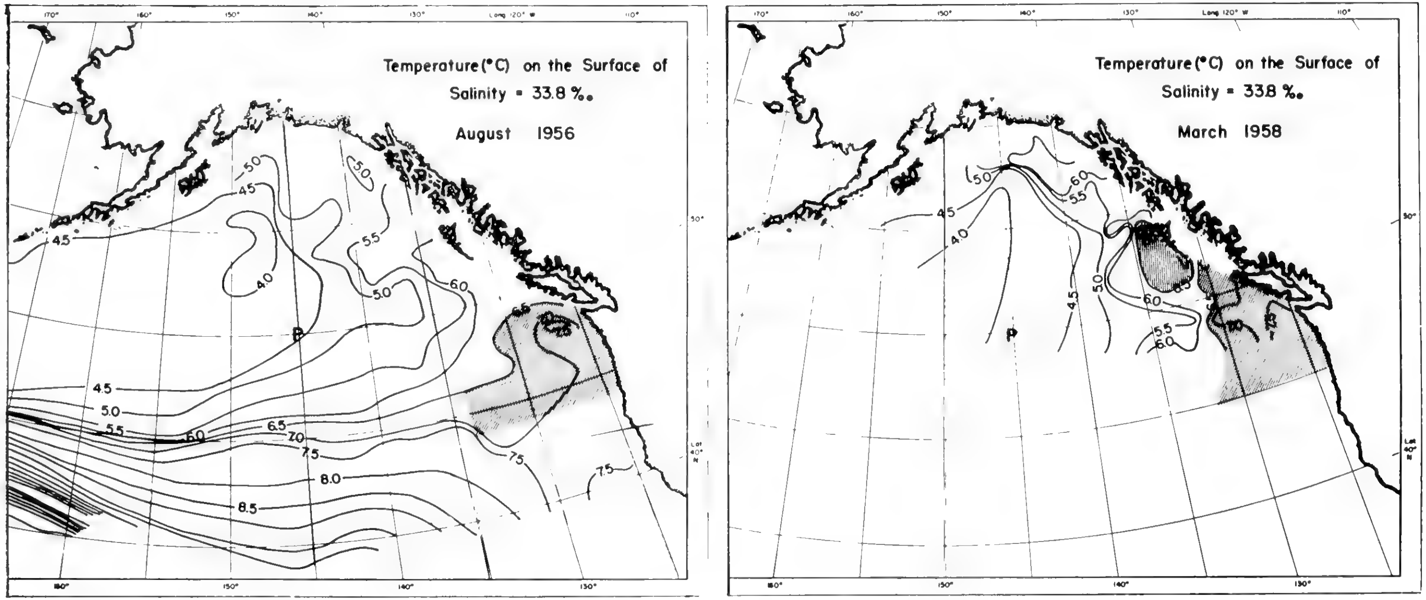


Fig. 10. (*Continued on facing page.*)

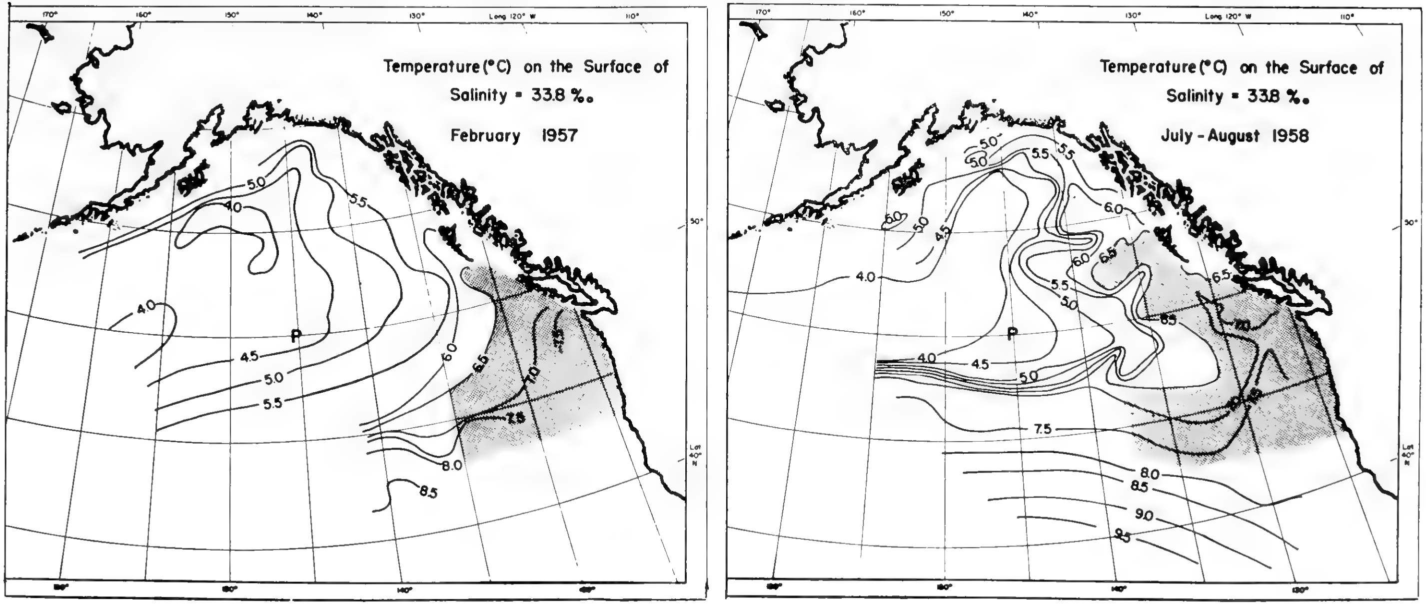

Temperature (°C) on the Surface of Salinity = 33.8 ‰
February 1957
Temperature (°C) on the Surface of Salinity = 33.8 ‰
July - August 1958
170°
160°
150°
140°
130°
Long 120° W
110°
50°
Lat 40° N
P
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5

Fig. 10

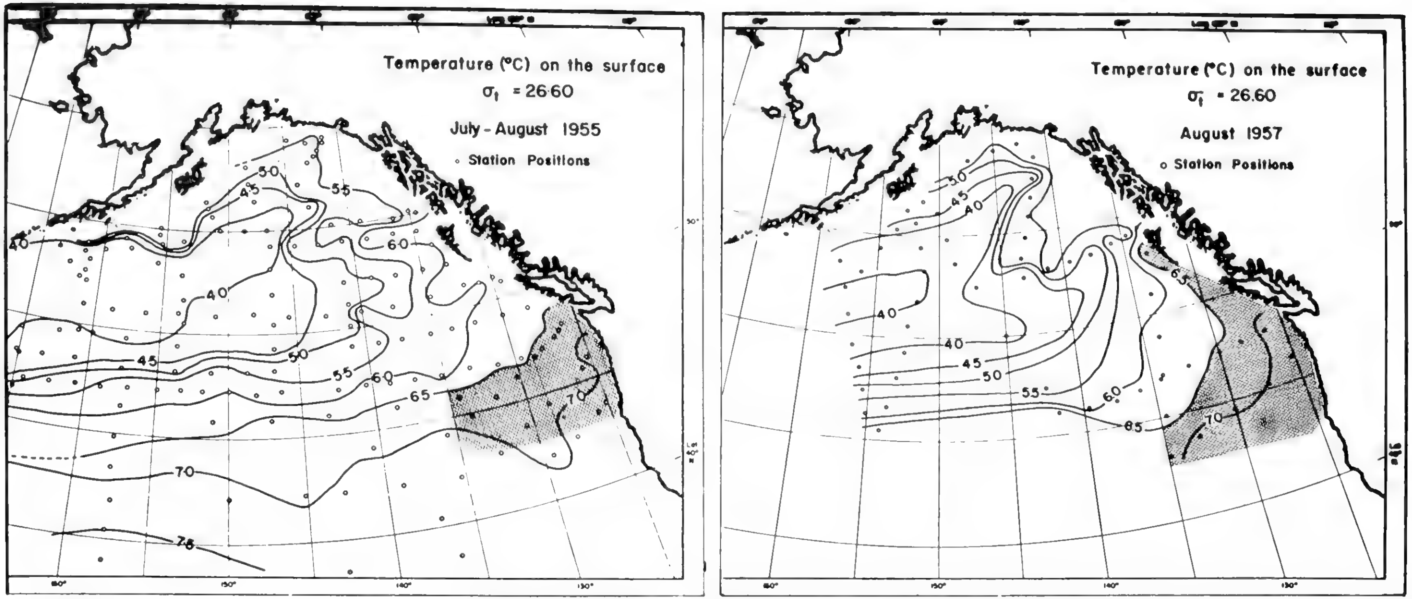


Fig. 11. *(Continued on facing page.)*

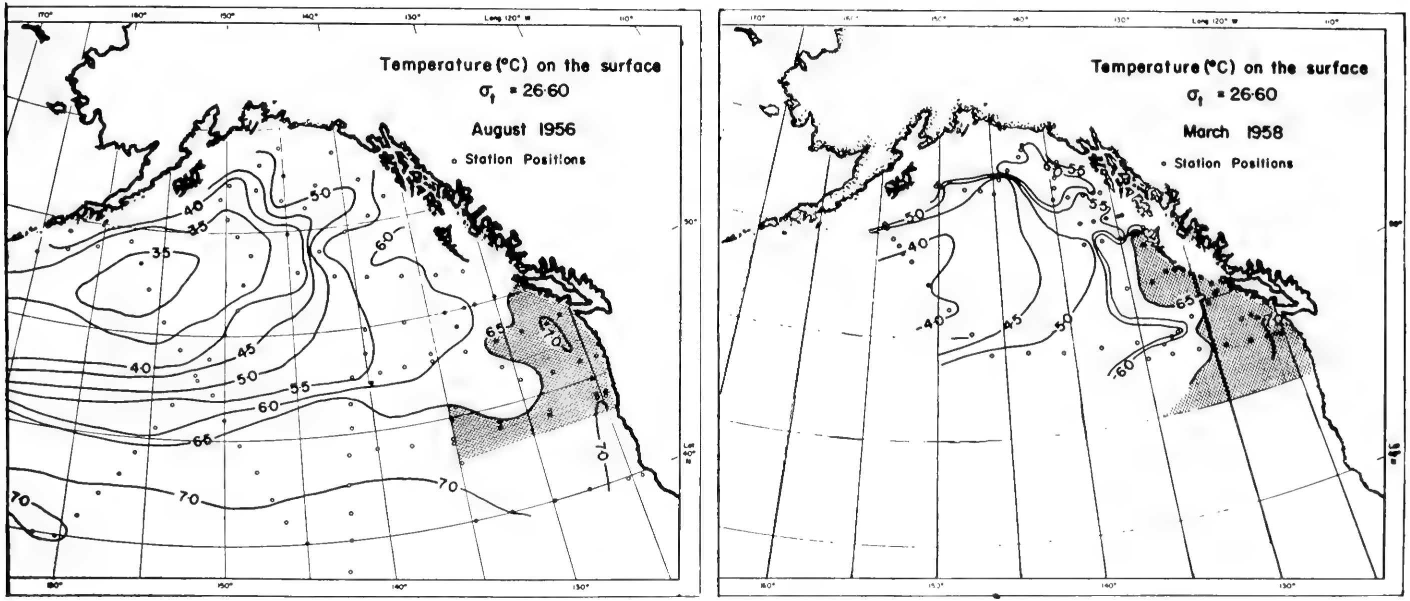


Fig. 11. *(Continued on following page.)*

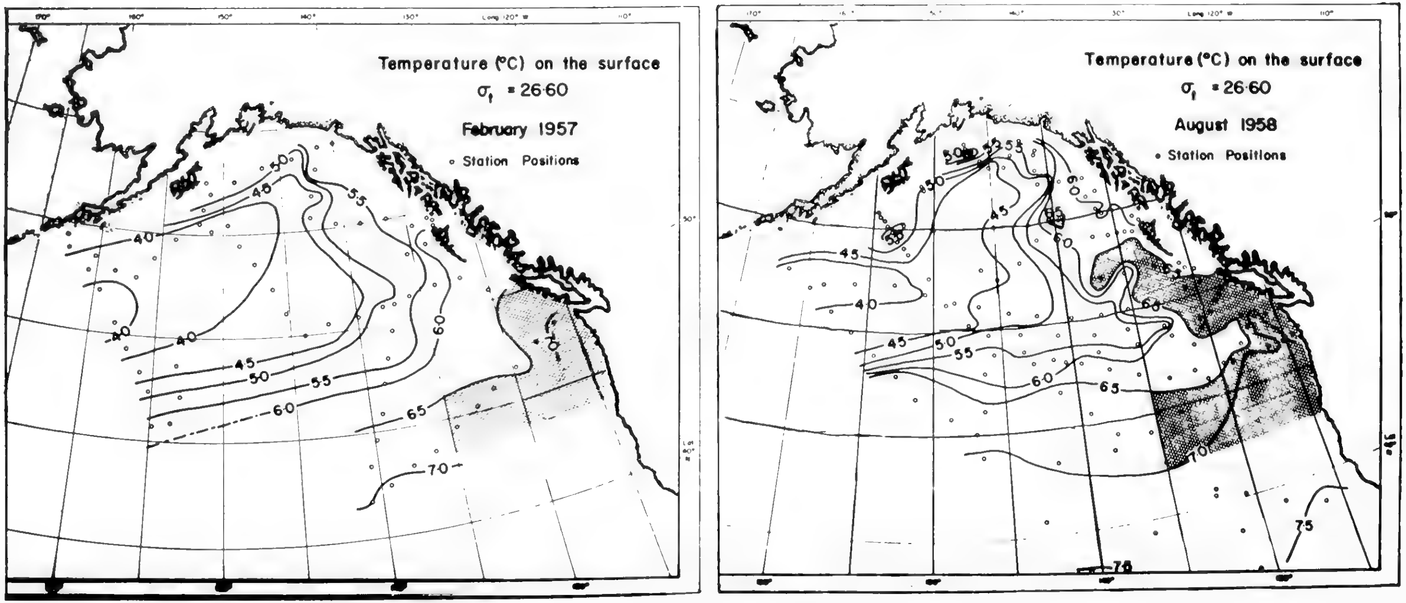

Temperature (°C) on the surface
σt = 26·60
February 1957
Station Positions
4·0
4·5
5·0
5·5
6·0
6·5
7·0
Long 120° W
Temperature (°C) on the surface
σt = 26·60
August 1958
Station Positions
4·0
4·5
5·0
5·5
6·0
6·5
7·0
7·5

Fig. 11

Tully *et al.* (1959) studied this phenomenon and showed that the temperature increase associated with the intrusion extended from the surface to nearly 500 m depth. They depicted the extent and advance of the intrusion by plotting temperature on the isopycnal sheet $\sigma_t = 26.60$ (Fig. 11).* In the eastern sub-Arctic Pacific Ocean this sheet lies everywhere in the halocline. It is close to the lower limit and below seasonal influence near the American coast, and approaches the upper limit in the center of the Gulf of Alaska.

Comparison of Figs. 10 and 11 shows that the halocline and isopycnal analyses coincide in every principal feature. In particular the progressive increase of the northward intrusion of warm water past the Canadian coast through 1957 and 1958 is equally apparent in both analyses. It may be argued that the interpretation in Fig. 10 is the more significant because it defines the features on the interzone boundary, a surface of known consistent upward transfer.

Acknowledgment

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* The anomaly of specific gravity, $\sigma_t = (\text{spec. gr.} - 1)1000$, hence $\sigma_t = 26.60$ corresponds to specific gravity 1.02660 (Sverdrup *et al.*, 1942).

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Length of Pelagic Larval Life in Marine Bottom Invertebrates as Related to Larval Transport by Ocean Currents

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IN 1904 Professor J. Stanley Gardiner published a most stimulating little paper on the distribution of larvae of marine animals in which he discussed the duration of pelagic larval life within different animal groups and the velocity of the surface currents, by which they might be transported over the oceans. He suggested that there are no barriers for many crustacean larvae. He estimated the maximum regular passage of larval echinoderms and enteropneusts at about 20 days, while for sipunculids, annelids, and molluscs it is progressively less, not more than 4 to 5 days for Müller's larvae and "regular planulae" and probably much less in many forms. Gardiner (1904, p. 409) concludes: "that in the present stage of knowledge any consideration of larval distribution is premature and must be inconclusive."

Gardiner seems to have had only a few data on the duration of pelagic larval life at his disposal. From rearing experiments he indicated a pelagic larval life of 34 and 32 days respectively for the sea urchins *Strongylocentrotus* and *Echinus*. These are the only figures he gave. If Gardiner had examined all the literature published up to 1904, he might have found figures for the duration of pelagic larval life for 1 polychaete, 1 asteroid, 3 echinoids, 1 prosobranch, 1 lamellibranch, and 5 decapod crustaceans, i.e., 12 species in all.

Now, 55 years later, there are fairly reliable data on the duration of the pelagic larval life for some 195 species, comprising polychaetes, asteroids, ophiurans, echinoids, holothurians, prosobranchs, lamellibranchs, and decapod crustaceans, and perhaps data for some 25 more species may be found in literature, so far not available to the present author. Also knowledge of the direction and velocity of the oceanic surface currents, which may transport the pelagic larvae, has increased considerably since Gardiner's time. It therefore seems reasonable to reexamine the whole question, the more so since larval transport by currents is regarded as an important means of distribution in nearly all papers and books discussing marine zoogeography (see, for instance, Ekman, 1953).

It must, however, be stressed, that this does not mean that the whole question is solved now. Many problems are still unsolved, but so many new facts have been brought together that it seems worth while to review present knowledge to find out what actually is known and what points must be tackled in the years to come in order to make the best progress.

The chief problem, which we shall consider, is to what extent surface currents may transport the larvae of coastal forms (i.e., of forms not able to reproduce beyond the limits of the continental shelf) across the ocean from one continent to another, from one continent to a group of islands, from one group of islands to another group, etc., thus introducing new faunal elements in already well-established communities beyond their normal boundaries. To examine these questions it seems reasonable first to get some idea about the length of pelagic larval life in the different groups of bottom invertebrates, then to collect similar information on the velocity of the most important surface currents crossing the oceans, and finally, to compare and discuss the two groups of information obtained.

As is well known, nearly all invertebrate species living in the Arctic and Antarctic coastal zones as well as all inhabitants of the deep sea seem to have a nonpelagic larval development. In cold temperate seas, for instance the waters round Denmark and Scotland, about 65 per cent of all species of bottom invertebrates have pelagic larvae, and in the tropical coastal areas pelagic larval development will be the rule in about 85 per cent of all species of bottom invertebrates (Thorson, 1950). Since, furthermore, the total number of species of marine coastal-dwelling invertebrates, especially the epifauna species, increases enormously from the Arctic toward the Tropics (Thorson, 1952), it is obvious that by far the best chances for long-distance larval transports exist in tropical regions.

Three main types of pelagic invertebrate larvae are known. One of these, which has a pelagic life of a few days to a few hours, may be disregarded here. The types which are of interest in our problem are the following.

The *lecithotrophic* pelagic larvae develop from fairly large, yolky eggs. They do not feed on the plankton, but rather exclusively on yolk within the egg cell from which they originate. This larval type accounts for about 10 per cent of the species with pelagic larvae in temperate as well as tropical sea areas. In most cases their pelagic larval life is fairly short. In a few cases, however, they may have a pelagic life of up to two months, and, if so, they must be considered in our calculations.

The *planktotrophic* larvae with a long pelagic life originate from small eggs with little yolk, and are often produced by the mother animal in huge quantities. They are known in the literature under the names veliger, tornaria, pilidium, trochophora, etc. They derive all or nearly all their food from the plankton and thus are fully dependent on the food conditions there. This larval type is found in more than 70 per cent of all marine invertebrates in recent seas, and it is this larval type which predominates in all speculation on larval transports. It also is among the parent animals giving rise to this larval type—and only there—that we find those enormous numbers of eggs per female per season (some 1100 to 500,000,000 eggs or more, average about 1,000,000 eggs) which seem to be of fundamental importance as a counterbalance to the great loss of larvae during a long pelagic life (Thorson, 1950, 1952).

For the present purpose, it seems less important to study the length of pelagic larval life within such groups or species, the adults of which are sedentary (cirripeds, serpulids) or sessile (actinians), since they may easily be transported over the oceans by other means than larval drifts, for instance by driftwood and, in our time, to an increasing extent, by ships or, in certain cases, even on the pontoons of hydroplanes. Sedentary species often have a more or less developed brood protection of the early larval stages, and in such cases larvae may be ready to hatch in a fairly advanced stage, to metamorphose and settle when the ship arrives in a new harbor. This significantly improves the chances for dispersal of the species concerned.

When, later on, we compare the figures for pelagic larval life and the chances for current transport in the individual species, we must realize that the animals may have obtained their recent pattern of distribution by several other means than larval transports: crabs may be dispersed on fouling sides of ships (Bertelsen and Ussing, 1936) or in ballast tanks (Peters and Panning, 1933), egg capsules of prosobranchs on sides of ships or in cargoes with living oysters (Chapman and Banner, 1949), etc. It will take too long to consider all these means of transport, but they must not be forgotten in our calculations, and it must also be kept in mind that most modern ships crossing the oceans will in one or two hours travel the same distance as does the average surface current in about twenty-four hours. Therefore, invasions of new species by ships may in future severely obscure the picture of natural dispersal of marine invertebrates.

The figures, which I have brought together so far for the duration of pelagic larval life in 195 species of bottom invertebrates are mostly based on rearings in *aquariums*, though a fair percentage of them originate from observations in *nature*. It has, however, been stressed by several biologists that in most cases development under laboratory conditions will advance more slowly than in the sea, the larval life thus being longer than the average one. Most laboratory experiments are, however, carried out at room temperatures, which are often some 2 to 5 degrees centigrade higher than the temperature of local sea areas at the same season. Thus, the higher temperatures accelerating the development, and the artificial aquarium conditions postponing development may counterbalance each other to give a final figure, which roughly and for all the larvae will hardly deviate much from the average figures in nature. In such species, where control observations on larval development made under natural conditions are compared with aquarium experiments, the results do not in most cases differ much. We also know about rearings in aquariums for which the rate of development was more rapid than in nature. So, taken as a whole and roughly, it seems that the figures obtained from laboratory experiments may give a fairly correct picture of the average rate of development.

Furthermore, it must be kept in mind, that figures from such laboratory experiments, for the present calculations, have been accepted only if the larvae were reared to their very oldest stage or through metamorphosis in a healthy state; for our purpose, what is most important to know is how slowly the larvae may develop without losing their ability to settle and metamorphose in a healthy state. So, what we must look for in the literature is the longest duration of the pelagic life of each individual species, which results in a successful settling and metamorphosis. If, for example, it is indicated for a larval species, that it may metamorphose within a space from 3 to 6 weeks after hatching, this will in the author's calculations be regarded as a 6-week pelagic life, since at least some of the larvae may be transported by the currents for that space of time.

We shall soon have to note other sources of error, but let us first look at Fig. 1, based on figures for 195 species of larvae. The data for this were brought together from about 300 different papers, but it does not seem reasonable to give all these references in a review paper such as this. All data for the diagram are, however, available in the author's files and he will gladly forward them to those who are especially interested. To the left are the systematic group and the number of species examined. The number of weeks from hatching to metamorphosis is given at the top and the black blocks show the percentage of all species examined within each group, which metamorphoses within each of the weeks indicated above. At the bottom the hatched block (in double scale) gives the total for all larvae. From this we may conclude, first, that about 70 per cent of all pelagic larval species examined thus far will on an average metamorphose and settle after less than 5 weeks of pelagic life, while about 80 per cent of all larvae will settle after less than 6 weeks of pelagic life and 86 per cent after less than 8 weeks of pelagic life. Or, to put it in another way, only

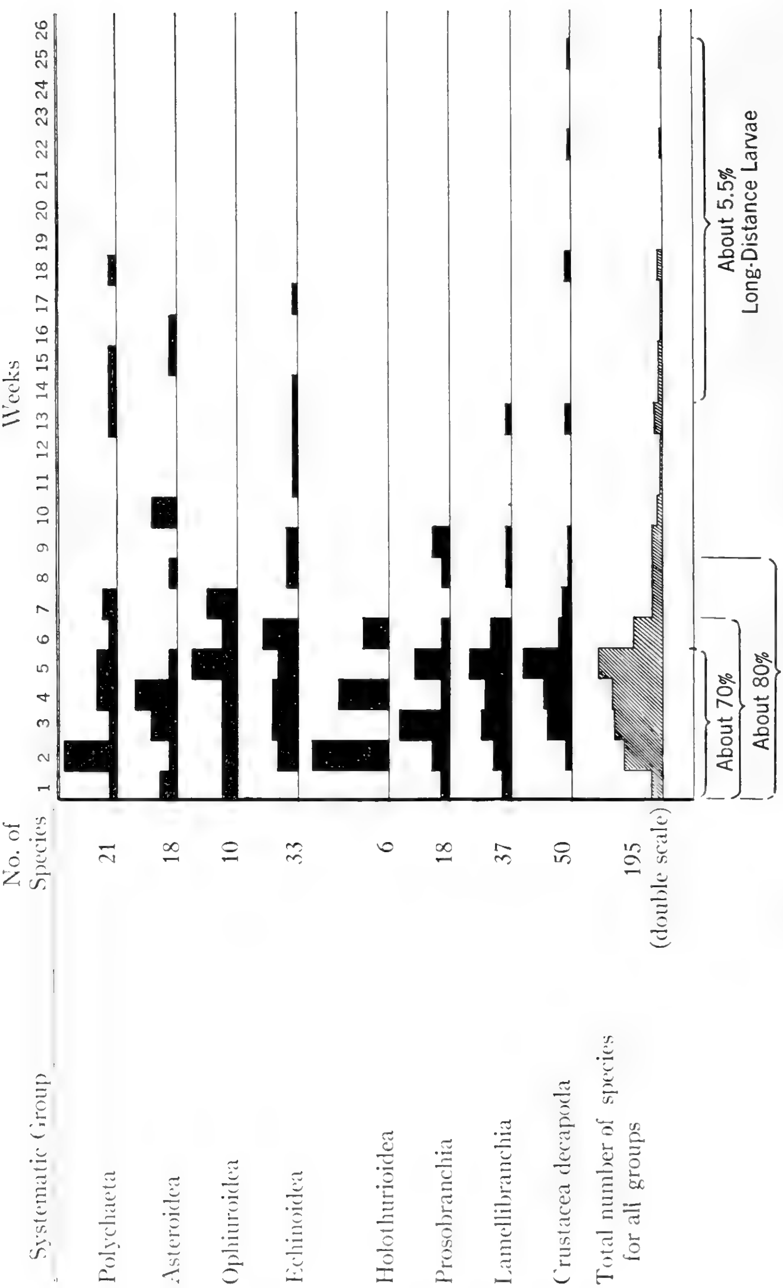

Fig. 1. Length of pelagic larval life, in weeks, for 195 species of marine bottom invertebrates.

5.5 per cent of all larval species examined thus far remain in the plankton for a period longer than 3 months. Only the last category may be regarded as true "long-distance larvae," which have to be considered as the chief objects for transoceanic transport. The diagram also shows that some systematic groups, as far as the species examined are concerned, have no long-distance larvae at all. This is the case for the ophiuroids, the holothurians, the prosobranchs, and the lamellibranchs, whereas polychaetes, asteroids, echinoids, and especially decapod crustaceans have at least some species which can be transported over wide areas.

If we return now to the sources of error of this diagram, some will want, no doubt, to stress the enormous variability in the length of the pelagic larval life as related, for instance, to temperature. A few examples will demonstrate this. In the sea urchin, *Evechinus chloroticus*, the length of the pelagic larval life may vary from 6 to 17 weeks (Mortensen, 1921; Maxwell, 1957). In the oyster, *Crassostrea virginica*, the larval life may vary from about 7 days at 24–27° C to 21 days at some 18° C (J. Nelson, 1908; T. C. Nelson, 1928), and Dr. Loosanoff (verbal information) has found that *Venus mercenaria* may vary the length of its larval life from 7 to 20 days. In the lobster, *Homarus americanus*, the larval life may vary from about 9 to 11 days at 22–23° C to 15 or 16 days at 18–19° C (Hadley, 1906; here taken from Ehrenbaum, 1907), and according to Templeman (1940) even from 14 days at 21° C to 49 days at 10° C.

Dr. Costlow and Dr. Bookhout (verbal information) have shown that the pelagic larval life of several species of crab larvae in rearing experiments in North Carolina may vary from 15 up to 40 days in the individual species according to the ecological conditions.

If we now use this information for Fig. 1, the following may be deduced. There is no reason to believe that the durations of pelagic larval life given in this diagram are minimal values. On the contrary, they seem to give average or perhaps a bit higher than average values. So, even if it is assumed that extraordinarily low temperatures, poor food conditions, etc., on certain occasions may prolong significantly the larval life, there is certainly no reason to believe that the figures given in the diagram have to be more than doubled—and hardly that. If now, to be certain, the figures are doubled, the conclusion will roughly be about the same as without doing so, namely that 80 per cent of all larval species examined so far will spend less than 6 × 2, i.e., 12, weeks in the plankton, which is too short a stay to make them long-distance larvae. A few figures will support this view. A surface current of average velocity will take some 22 to 23 weeks to pass from Cape Hatteras to the Azores, some 19 to 20 weeks to pass from Somaliland to the west coast of India, and some 19 to 20 weeks to pass from the coast of Costa Rica to Clipperton Island, that is, much longer lengths of time than are available to 80 per cent of all larval species, even if the figures in the diagram are doubled. However, if we consider that twice the time given in Fig. 1 is possible under certain circumstances, then a 10- to 12-week larval life may very well give the common larval types a chance to cross, for instance, from East Africa to the Seychelles, from the Seychelles to the Chagos Islands, from Ceylon to the Maldives or, in many cases, from one island group inside Oceania to its neighbor group. But this is not what is understood by transoceanic long-distance transport.

All this smells very much of statistics, and since we are much more interested in the living larvae in the plankton than in diagrams, we had better return to the individual larval groups to see what they actually stand for. The values in Fig. 1 are fairly close to average ones, and the speed of the surface currents, with which we have tried to compare our figures for larval life, are also based on average velocities. What we should actually like to know is the maximum length of pelagic life which any larva will be able to spend in the plankton finally leading to a successful metamorphosis, and the maximum velocity of the ocean-crossing surface currents in a year especially favorable for larval transport. In other words, we should like to know how long a distance the larvae may be transported during a season in which a maximum length of pelagic life and a maximum current velocity occur at the same time. We must realize that even if such a favorable condition of maximal length of larval life and maximal current velocity might occur, for instance, only once in some hundred years, this might be sufficient for a larval swarm to conquer new coastal zones, to gain a foothold there, and to found a permanent population. Actually, the recent pattern of distribution of marine coastal faunas represents the accumulation of all "transport miracles" during thousands of years, and our larval transport problems have to be considered with this in mind.

Let us for a moment return to the larvae, first to the *polychaetes*, which are known to be very cosmopolitan. When comparing the number of polychaete species from western Europe with those of the Indo-Western Pacific area, you will find that some 30 per cent of the species are common to both, whereas the distribution of common species in such groups as echinoderms, prosobranchs, and lamellibranchs is less than 2 per cent. This seems mainly to be due to the fact that the individual polychaete species (in contrast to species of the other groups mentioned) may vary the mode of reproduction from pelagic to nonpelagic, etc., according to the season and locality. Thus they are always able to respond in the most favorable way to ecological conditions (Thorson, 1950, p. 32). In some cases, long-distance larvae also may have contributed to the cosmopolitan success of this group. At least it is a fact that such species of polychaetes which actually have long-distance larvae: for instance *Polydora ciliata* and *Chaetopterus variopedatus* also have a worldwide distribution. Polychaete larvae seem to have better conditions for long-distance transport than most other groups. Day (1937) and Wilson (see his review of the whole problem, 1952) have clearly shown the ability of polychaete larvae to postpone their metamorphosis for days and even up to several weeks until they reach a substratum suitable for metamorphosis and settling. Even when the metamorphosis cannot be postponed any longer, some of these larvae may metamorphose in "mid-water" to continue the planktonic life as "pelagic bottom stages." The "Benham stage" of *Arenicola* is probably such a mid-water metamorphosis. All in all, polychaete larvae thus seem to have still better chances for long-distance transport than is immediately seen from Fig. 1.

The *asteroids* on the average have a fairly short pelagic life, but species of the genera *Astropecten* and *Asterias* may have a larval life of 15–16 weeks. The longest larval life among asteroids seems, however, to be found in some species of the genus *Luidia*. Thus, the larva of *Luidia sarsi* may attain the remarkable length of 25–35 mm (Mortensen, 1901) and seems fit for a long pelagic life, the duration of which has not been ascertained thus far. For *Luidia ciliaris*, the egg number of a single female has been calculated at 200,000,000 at least (Mortensen, 1913), a figure which suggests a heavy loss of larvae, and this again is normally closely associated with a long planktonic stage. In accordance with these suggestions it seems reasonable to point out that a species of *Luidia* (*L. senegalensis*) actually is found on both shores of the tropical Atlantic Ocean, off Senegal and off Brazil (Hyman, 1955).

This distribution pattern seems to lose its value as an argument when we realize that a fair number of *ophiuroids* are also common to West Africa and the Antilles (Hyman, 1955). Figure 1 shows that of the ten species of ophiuroids examined so far, all tend to have a very short pelagic life. To explain this apparent contradiction, I should like to call attention to some observations on larval asteroids and ophiuroids, so far disregarded by all textbooks, but probably of great importance. In 1906 Delap observed that the giant, 25–35 mm long, larval body of the sea star, *Luidia sarsi*, survived for at least 3 months after the young bottom stage had developed from it, metamorphosed, and settled. In most other asteroids the larval body will not exceed 2 mm in length, and a biologist rearing asteroid larvae will hardly pay any attention to the larval body after the settling of the young bottom stage. In *Luidia*, the larval body is so conspicuous that one may hardly disregard it, and it has been found to live for at least 3 more months. This was confirmed by Tattersall and Sheppard (1934).

Still more surprising is a discovery made by Mortensen (1921), carefully hidden in his long paper on echinoderm larval development. In it (pp. 147–149) he describes an ophiuroid larva, *Ophiopluteus opulentus*, from Thailand which, in his rearing dishes, after it had produced and given off one young bottom stage, regenerated its ciliary bands, its mouth, and esophagus to look like a completely normal larva before the development of the young bottom stage set in. Since Mortensen was a most reliable and careful observer, I should like to quote him. He concludes this exciting observation by stating: "there seems no reason to doubt that a new complete and ultimately metamorphosing larva may be the result. Thus we would here have a true case of metagenesis, otherwise totally unknown in Echinoderms."

I should not be surprised at all, if such a metagenetic larval development would prove to be a common mode of reproduction in some tropical ophiurans and perhaps also in some sea stars. Who knows? Nobody has ever looked for it! If Mortensen is right, the ophiopluteus must be regarded as an asexual polyp, producing sexual bottom stages and, what is of special interest for our problem, the larval life may be prolonged to an unknown extent. But even if such a "budding" from the tropical brittle star larvae might be regarded as an exception, not the rule, it might very well give some of the billions of brittle star larvae drifting away in the water masses a chance to cross the wide ocean basins. This is actually what it seems to have done. Hyman (1955) mentions seven species of ophiuroids common to the tropical Pacific-Panama region and to the Indo-West Pacific and (or) Oceania, and she adds: "Ophiuroids thus appear to have been more successful than other echinoderm groups in migrating from the Indo-Pacific to the western shores of tropical America."

Also without assuming this new and sensational mode of dispersal, larval asteroids and larval ophiurans have significantly better chances for long-distance transports than indicated in the diagram. They are known to metamorphose very often in mid-water, which might prolong their pelagic life to a considerable degree—how much, we do not know.

The *echinoids* often have a fairly long pelagic life. *Arbacia punctulata* has a larval life of up to 97 days and *Evechinus chloroticus* up to 116 days. In echinoids, the larval body is, however, completely destroyed by metamorphosis (verbal information from Professor L. von Ubisch), so that a "budding" like that suggested for ophiurans and asteroids cannot help to prolong larval life. Mid-water metamorphosis and postponement of metamorphosis until the right substratum is encountered is, however, a common occurrence among echinoids and may considerably prolong their pelagic life. Nevertheless, true long-distance larvae will hardly be found within this group, and it is, in good agreement with this statement, that the tropical West and East Pacific coasts have no echinoid species in common (Ekman, 1953; Hyman, 1955).

The holothurian diagram, based on only six species, is disregarded, and we turn to the *prosobranchiate gastropods*. As seen from Fig. 1, the pelagic life is very short, no species so far examined having a longer stay in the plankton than 9 weeks. The shells are heavy, the veliger larvae retract within their shell at the slightest disturbance and then sink toward the bottom, which slows down transportation. Mid-water metamorphosis also seems to be unknown. Thus, for the usual type of prosobranch veligers, the chances for larval transportation are limited to only very short distances. However, we know also of groups of pronounced long-distance larvae among prosobranchs. They are not indicated in the figure simply because, thus far, they have never been reared through metamorphosis under controlled conditions.

Recent studies have shown that such genera as *Cypraea, Lamellaria, Tonna, Cassis, Charonia, Cymatium*, and *Bursa* have larvae hatching as tiny veligers, which live long and grow vigorously during their pelagic phase and often do not leave the plankton until their shells are 4 to 5 mm long. They have 4 or more (up to 12) enormous velar lobes (Fig. 2), and several of them have been found midway across the oceans. The eggs are laid by the parents in huge quantities, and the younger larvae show another feature, making them fit for a long planktonic life, i.e., long spines on the shell which may protect them against enemies and help them to reduce significantly loss during their stay in the plankton (see Dawydoff, 1940; Lebour, 1945, p. 483, Fig. 34). The length of pelagic life in these genera is not known; I should guess that it might last for some 6 months. They are true long-distance larvae, able to cross the oceans, and just within these genera we know of a long series of circumtropical species, clearly proving the efficiency of larval transport.

The *lamellibranchs* normally have a very short pelagic life. The longest larval life is 86 days for *Mytilus crassitesta* from Japan, 80 per cent of them metamorphose and settle earlier than 5 weeks after hatching. Like the gastropod veligers, their shells are heavy; the velum is withdrawn when they are disturbed, which makes them sink toward the bottom and counteracts transportation.

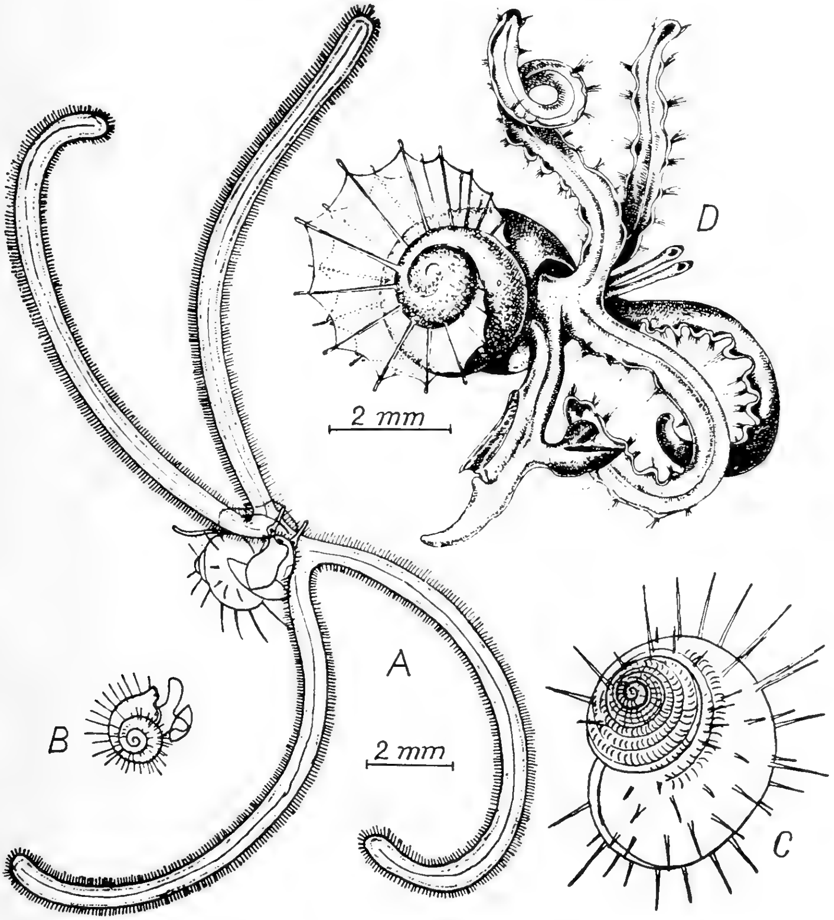

Fig. 2. Prosobranch larvae of the long distance type. *A*, *B*, and *C*, larvae of *Tonna* sp. taken off Bermuda (Lebour, 1945); *D*, larva of unknown prosobranch from the China Sea (Dawydoff, 1940).

Mid-water metamorphosis is rare. Their chances of dispersal are hardly better than indicated in Fig. 1, and even transports over fairly small sea areas may be a serious problem. It is in good agreement with Ekman's (1953, p. 19) statement for Hawaii that "especially the mussels are largely endemic." Among all the groups studied this seems to be the one most unfit for long-distance transportation.

In *decapod crustaceans* the majority of the larval species also have a short planktonic life, 70 per cent requiring less than 5 weeks for their pelagic development. Among the species with short planktonic stages are all the crab larvae examined thus far. The long-distance larvae seem to fall in only three groups: the Pandalid shrimps, which can also swim as adults, the *Hippa* or *Emerita* group, and especially the spiny lobsters, *Panulirus*. *Hippa*s have a pelagic life from 90 to 120 days, but since they often live in areas where the currents move parallel to or along the coast, their chances for transportation are reduced (Johnson, 1939). The *Panulirus* group, however, with a pelagic life of 150 to 180 days, has true long-distance larvae, a fact which is in good agreement with its wide and often circumtropical distribution (Chace and Dumont, 1949).

The currents, which have been considered here are only the *surface* currents. We know that nearly all larvae are photopositive just after hatching and rise to the surface. We also know, however, that when approaching metamorphosis they become photonegative, thus approaching the bottom substratum, where they will settle (Thorson, 1946; 1950). But these vertical migrations seem to take place only within one and the same water mass. Most larvae are, so to speak, "born into a certain water mass and seem, also when transported by the current, to regulate themselves up and down so as to stay more or less within it during their whole pelagic life (Banse, 1955, 1956). Thus, their photonegativity in the older stages will hardly stimulate them to cross a discontinuity layer. If a surface layer has a thickness of, for instance, 300 m, the young larvae may be found at the surface, the older near 300 m depth, but normally not deeper.

For our purpose, currents which run parallel to the coastal lines (the Humboldt, Benguela, Agulhas currents, etc.) are of less importance. Even the Arctic currents running mostly parallel to the continents and in a region where only a very few species reproduce by pelagic larvae may be disregarded here. Therefore, only currents *crossing* the oceans have been considered in these calculations.

Examples have already been given to demonstrate that a rise in temperature will shorten the pelagic larval phase. This again means that a current which is gradually heated on its way over the oceans (for instance currents running from West Africa toward Brazil and the Antilles) will carry the larvae a shorter distance than currents which are gradually cooled (i.e., the Gulf Stream)—perhaps a fact of much significance.

Figure 3, in which an attempt has been made to combine the average velocity of ocean-crossing surface currents (here indicated through the number of weeks used to pass a known distance) with the time spent by the larvae in the plankton, is based upon all available information including the most recent British and American pilot charts. The current velocity has been calculated for the seasons of the year when each current is most direct and most rapid. In some cases the currents for the northern summer (S) as well as the northern winter (W) are indicated. The numbers referring to the currents are given to the left, first for the Atlantic Ocean, next for the Indian Ocean, and finally for the Pacific Ocean. Within each of these areas the currents moving from east to west are given first. At the top are figures to indicate the number of weeks used for the current to flow the indicated distance. The deadlines for pelagic life in 70 per cent (dotted line) and 80 per cent (solid line) of all larval species examined so far have been indicated. The hatched area shows the number of weeks during which even long-distance larvae tend to metamorphose and disappear from the plankton.

It will be seen that under average conditions even most long-distance larvae have a much too short pelagic life to survive the critical distances across the eastern Pacific (i.e., from Galápagos to Christmas Island or from Mellish Bank to California), and even the most rapid currents from West Africa to Brazil and the Antilles will in most cases be too slow even for long-distance larvae.

These current calculations are based on *average* velocities, and what we are interested in is the *maximum* velocity within a space of some hundred years. It is well known from old measurements that the Gulf Stream, for instance, may vary its velocity significantly not only during the course of a year, but also over long periods of time. On the assumption that such optimal conditions might now and then occur within some hundred years, there is hardly any doubt that the true long-distance larvae may sometimes have opportunities to cross even the eastern Pacific, and, under

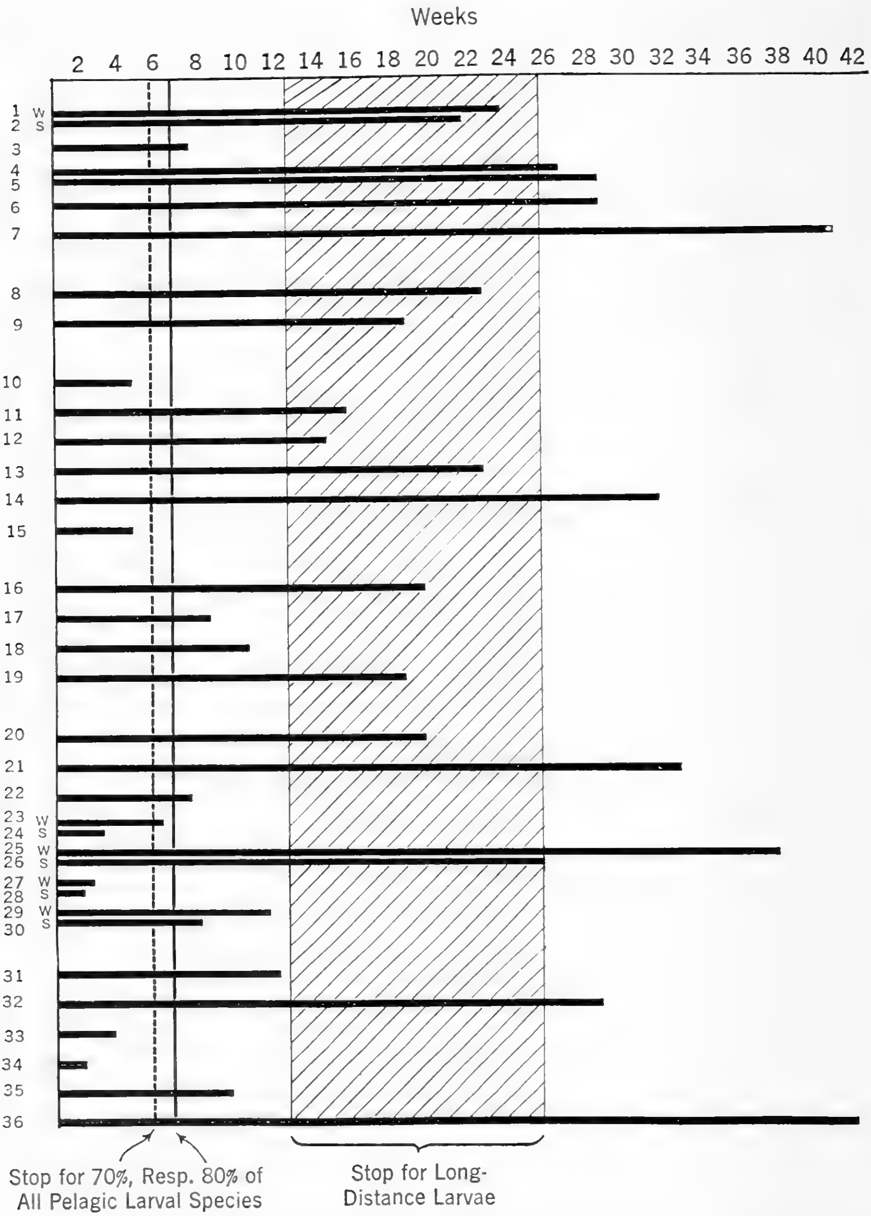

Fig. 3. Number of weeks used by the most important ocean-crossing surface currents to pass from coast to coast in relation to the length of pelagic larval life of bottom invertebrates (coastal forms). (Explanation on facing page.)

the same conditions, it also seems likely that several other species of pelagic larvae, though not of the long-distance type, may get some chances to spread from island group to island group inside Oceania.

Explanation of Fig. 3

Atlantic Ocean, east to west (1–7)

1–2, West Africa (0° Lat) to St. Paul Island, about 4500 km or 2430 miles; 3, St. Paul Island to Brazil (5° N Lat), about 2670 km or 1450 miles; 4–5, West Africa (5°–10° S Lat) to Fernando Noronha, about 5100 km or 2760 miles; 6, Cape Verde Islands to Southern Antilles, about 3670 km or 2000 miles; 7, Canary Islands to Southern Antilles, about 5100 km or 2830 miles.

Atlantic Ocean, west to east (8–9)

8, Cape Hatteras to the Azores, about 4000 km or 2150 miles; 9, Equatorial countercurrent about 3630 km or 2000 miles.

Indian Ocean, east to west (10–15)

10, Ceylonto Maldives, about 1300 km or 750 miles; 11, Maldives to East Africa 2° S Lat), about 2530 km or 1350 miles; 12, North Australia (130° E Long, 12° S Lat) to Cocos Islands, about 2420 km or 1300 miles; 13, Southwest Australia to Cocos Islands, about 2900 km or 1570 miles; 14, Cocos Islands to Saya del Malha Bank, about 4100 km or 2200 miles; 15, Saya del Malha Bank to North Madagascar, about 1080 km or 580 miles.

Indian Ocean, west to east (16–19)

16, Somaliland (12° N Lat) to Maldives or west coast of India, about 3300 km or 1780 miles; 17, East Africa (5° S Lat) to Seychelles, about 1650 km or 890 miles; 18, Seychelles to Chagos Islands, about 1650 km or 890 miles; 19, Chagos Islands to West Sumatra, about 3000 km or 1600 miles.

Pacific Ocean, east to west (20–30)

20, Costa Rica to Clipperton Island, about 2500 km or 1350 miles; 21, Clipperton Island to North Central Sporades, about 5170 km or 2800 miles; 22, North Central Sporades to Keats Bank and Marshall Islands, about 2750 km or 1480 miles; 23–24, Peru to Galápagos Islands, about 880 km or 475 miles; 25–26, Galápagos Islands to Christmas Island, about 7150 km or 3960 miles; 27–28, Christmas Island to Jarvis Island, about 300 km or 160 miles; 29–30, Jarvis Island to Howland and Baker Islands, about 1770 km or 955 miles.

Pacific Ocean, west to east (31–36)

31, Marshall Islands to North Central Sporades, about 2750 km or 1480 miles; 32, North Central Sporades to Clipperton Island, about 5170 km or 2800 miles; 33, Clipperton Island to Costa Rica, about 2500 km or 1350 miles; 34, East Japan Islands to Ganges Island, about 1440 km or 780 miles; 35, Ganges Island to Morell Island or Mellish Bank, about 2200 km or 1190 miles; 36, Mellish Bank to California, about 5450 km or 2950 miles.

Observations: *Surface* currents only.
W = northern winter; S = northern summer.
Miles = nautical miles, i.e., 1852 m each.

Only a fairly small percentage of the total Indo-West Pacific coastal fauna has reached Hawaii in spite of the chain of "strategically" placed islands along the southern border of the Kuroshio current, islands which might have been reached by several larvae at normal current velocities. This tends to show that in order to be of true importance as an intermediate station for larval transport, the areal extent of an island or island group must not be too small. It must be remembered that most larvae aggregate in the plankton; they are transported in swarms. If an island is very small, huge larval swarms may pass it a short distance away without contacting it. On the other hand, this aggregation may also prove extremely useful for the larvae. In several marine invertebrates a whole population will spawn epidemically (Thorson, 1946, 1950). Such a swarm of larvae, all from the same brood, is caught up in and drifts with the current, exposed to much the same conditions in the same water mass. In most cases the whole swarm will perish before reaching a new transoceanic coast. But *if*, for instance, once in some two hundred years, they are successful in crossing an ocean, then a *whole* swarm may arrive—enough to found a new population.

Summary

Eighty per cent of all bottom invertebrates with pelagic larvae have a planktonic life of less than 6 weeks. Even if the length of this stage is doubled or if the larvae are transported by especially rapid currents, they never seem to have even the slightest chance to cross the larger ocean basins.

The group that has the least chance for long-distance transport is the lamellibranchs. Polychaetes and echinoids include at least some species which have a fairly long stay in the plankton, although they cannot be regarded as true long-distance larvae. Some tropical ophiurans and perhaps also some tropical asteroids may have chances to cross even the widest ocean basins, provided that Mortensen's observation on the "budding larval polyps" holds true. True long-distance larvae (i.e., larvae directly "built" for long-distance transport) seem only to occur in special groups of prosobranchs and decapod crustaceans. They are equipped to stay for such a long time in the plankton that they may often with success bridge the enormous gap between oceanic coastal zones. True long-distance larvae, furthermore, seem mainly to be associated with tropical and subtropical seas and to be rare or lacking in temperate and cold regions.

The most urgent problems for study in the near future to improve our understanding of larval transport problems are the re-examination of Mortensen's observation on budding and metagenesis on several tropical species of ophiurans and asteroids and a valid series of figures for the maximum velocities of the ocean-crossing surface currents.

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Problems of Epicontinental Sedimentation

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THE term "epicontinental" has been used in various senses. Usually it is used to indicate marine sedimentation on the continental blocks, with the edge of the shelf taken as the outer limit, but the whole continental terrace may be included, and the outer margin may be placed where the deep-ocean floor starts. In the present symposium the latter meaning is used for the sake of convenience, although it is unusual.

The marine geologist attempting to understand all aspects of epicontinental sedimentation forthwith discovers that he cannot remain aloof from the traditional fields of the other marine sciences because geophysical, biological, chemical, meteorological, and dynamic oceanographical aspects are involved. This statement could be applied to almost any other problem of oceanology, and is so obvious in this age of specialization that it need hardly be emphasized. Nowadays other sciences must be consulted as an irksome duty, unless one is lucky enough to be a member of a team at a large oceanographic institute. A geologist is soon beyond his depth when entering the chemical or physical ocean, and it takes him a disproportionate amount of time to find the information he needs. Lack of insight or knowledge causes neglect or misuse of relevant matter and hence, there is a tendency to shy away from the border fields.

At the outset of a round table conference it should be helpful to focus attention on the overlapping fields and treat them as an opportune cause for interchange of thought. This is an ambitious task, and certainly I shall fall short of what you have a right to expect. Not only will you notice that salient problems are overlooked, but I am sure you will find also that available information is ignored. However, the more you realize the magnitude of the failure, the more stimulating this introduction should be for ensuing discussions. My theme will be also partly a plea for research into special problems, but it should be taken as a request to the nongeological oceanographer to offer reviews of knowledge already available on certain subjects and to present them in such a form that the geologist can follow the argument.

Exceptional Position of the Geological Oceanographer

In the brotherhood of oceanographers the marine geologist occupies a somewhat divergent position. It is important to point this out before starting a tour of inspection in the borderlands of his domain. All other marine scientists study their subject principally to learn more about the sea and its floor. The chance of physical or chemical oceanographers discovering something important to their mother science is remote. Their main reason for keeping in contact with developments in that branch of learning is to avoid missing new lines of attack or new techniques that can be applied to the ocean. The vast majority of biologists can ignore marine biology without fear of missing important developments in their own domain.

For the marine geologist, however, the stimulus to study the ocean originally came from hard rock geology, and land geologists always will continue to demand results of their marine colleagues. It is one of the major tasks of the stratigraphic geologist to read the facies of ancient rocks; this jargon means to deduce from the present properties and fossil content of a rock the conditions prevailing during sedimentation. As the vast majority of stratified rocks are of marine origin, the stratigrapher is constantly occupied with the study of former sea floors. Until about World War I he could not be bothered, and, especially, he could not afford to study the present sea floor, so he was wont to deduce from his rocks what submarine conditions must be like. The information he gathered from the present day seas was limited to beaches and the scanty results of deep-sea expeditions. The latter information has been mainly of negative value because it turns out that deep-ocean sediments are practically lacking on the continents.

As more information concerning the present sea floor became available, it was more and more obvious that at the present stage of development the most efficient procedure to gain an understanding of the facies of rocks would be to catch up on the investigation of the sea floor before attempting to decipher knowledge from the rocks themselves. At last this is happening, and almost invariably work at sea brings to light unexpected conditions. Most marine geologists have gone so far that they hardly look deeper inland than a beach of coastal dune. They have joined other oceanographers wholeheartedly in their mariner's life. The name often used for this type of work is "submarine geology," which lays stress on the underwater happenings, that is, on conditions below the surface of the present seas. The more general term "marine geology" can be considered as comprising also the application of submarine findings to ancient rocks, which is the main job of those marine geologists who have remained closer to the study of land geology. For both groups the keen interest in their results shown by fellow geologists on land, to say nothing of the funds provided by oil companies, form a major stimulus for these studies. Metaphorically, the nongeological oceanographer is a native of the oceans, the submarine geologist is an immigrant who still has many ties with his home country on land, and the marine geologist is a kind of science attaché on behalf of the stratigraphers. Admittedly meteorologists are in a somewhat similar position, with the difference, however, that very few of them specialize on land phenomena in their realm in the way most geologists do.

The fact that the geological oceanographer has ulterior motives in studying the sea must color his outlook somewhat. It is not enough for geologists to be able to tell where certain processes are taking place in the present oceans. We must understand why and also must know what are the limiting conditions if we are to be able to distinguish the diagnostic value of features in ancient rocks. It is obvious that the need for help from biological oceanographers has the same background, namely the wish to establish the relations between environment and biocoenosis for the instruction of the hard rock geologist.

I hope we shall be forgiven for the urgency with which we demand assistance in solving geological problems on account of the pressure put on us by our stratigraphic colleagues.

Sources and Movement of Sediment

As a basis for discussion the sources of sedimentary matter and the mechanisms of transport in the ocean are reviewed briefly. The atmosphere drops cosmic and windborne dust, partly of volcanic origin. The land contributes by volcanic activity, glaciers reaching the coast, ice floes, rivers, and coastal abrasion. Sea water is capable of providing sediment by evaporation or precipitation (clay?), from organisms, and by dropping clay particles that have floated around so long that their ultimate source on land can be disregarded. Finally the sea floor itself is a source of sedimentary matter. Authigenic minerals and concretions (nodules, glauconite, etc.) are formed. Submarine volcanoes add their products, and scarps can deliver blocks by crumbling, e.g., due to overthrusting. Currents and waves can erode recent or old material from the sea bed. Then two types of resedimentation, or "cannibalism," take place, one by sliding, the other by turbidity currents. In principle there is no difference between resedimentation and intermittent transport, but the former term implies a relatively long interruption or a change of mechanism.

Apart perhaps from the subject of clay flocculation and precipitation in its various aspects, the geologist can still feel that he remains within the bounds of his own subject when considering sources, but as soon as he starts to study transportation, he has to collaborate with physical oceanographers. An outline of the processes follows.

1. Transport without primary movement of sea water can be subdivided: (*a*) dropping from the air after transport in the atmosphere; (*b*) surface transport of suspended material in freshwater spreading over salt water or floating (pumice or dry grains); (*c*) rafting by ice or organisms (dead and alive); (*d*) origin from organisms that have moved more or less during their life time (planktonic, benthonic, nektonic); (*e*) sliding of sediment on steep slopes.

2. Transportation by ocean currents, to be subdivided into (*a*) tidal currents, especially in shallow water and in narrows; (*b*) seiches due to swinging water masses (nontidal); (*c*) wind-driven currents, either shallow and variable in force and direction or deep and more stable; (*d*) jet currents due to differences in level; (*e*) density currents due to differences in temperature or salinity, and turbidity currents due to the potential energy of suspended sediment seeking a lower level, under the influence of gravity.

3. Wave action: (*a*) undertow and rip currents with a distinction made between waves perpendicular to the coast, or oblique to the coast, or those combined with marine currents; (*b*) tsunamis in shallow water; and (*c*) internal waves at breaks in slope.

All data on the movement of water should prove useful to the sedimentologist, but the information geologists seek is mainly from the boundaries of the ocean, and it is my impression, entirely from the geological point of view, that physical oceanographers have concentrated on the wrong aspects. Waves have been studied at the surface, but where they change to surf and swash, the interest of the physicist apparently slackens. This is just where the destructive and transporting actions begin to become really exciting to geologists. The surfaec spread of freshwater has not received the attention it deserves from physical and chemical workers. They would greatly assist geologists by taking samples off the mouths of rivers in flood to find out how much and in what form sand, clay, and organic matter are carried, how these drop to the salt water, and how far they are transported out to sea.

Below the surface the action of waves on the bottom, for instance, the maximum velocities and movement of particles, is left almost entirely to the geologist to determine. Can sand be moved offshore near the depth limits of its disturbance or only inshore? How deep is this limit under various conditions of exposure? Repeatedly one hears of sand grains being caught in nets or bottles below the surface. This has been ascribed to attached bubbles, but is that not contrary to the principles of submarine navigation? An explanation and unquestionable quantitative data are urgent requirements, because sand grains are known to occur in deep-water deposits and must be accounted for in some way.

When the action of currents along the ocean bed is considered, there is the same failure on the part of the physical oceanographers to provide information. Current charts of the sea floor with as much detail as shown for the surface on navigational charts are needed. Obviously that need cannot be met until the future, but a few data to keep the geologists going in the meantime would be appreciated. Probably geologists are too vague when demanding information on bottom currents, but dynamic oceanographers should realize that data are needed to relate them with the sedimentation of clay or sand, current ripples, and nondeposition. It is knowledge of the speed and turbulence of the water actually in contact with the bottom that is required. Maximum velocities due to the combination of steady and oscillatory currents are also of the greatest importance.

Where is this need for bottom data most urgently felt? In the first place on the shelf, particularly near its outer margin where deposition is almost absent. What is the part played by long waves and tidal currents in this problem? Is the cause of clay sedimentation close to the shore due partly to a greater supply or only to less transport power? In shallow water even slight depressions tend to accumulate finer sediment than the surroundings. Is the protection thus proved more against wave action or against currents? Then there is a strong suspicion that in areas where *Globigerina* ooze is accumulating, clay sedimentation is being counteracted. This winnowing may go so far as to leave almost pure foraminiferal sand, whereas clay is accumulating in the more sheltered areas in the surroundings.

The "non-depositional" condition on guyots is another difficulty, and no explanation is yet available for Tertiary sediment lying bare or only slightly buried even on flat stretches of the deep-sea floor. Fishes and other animals brushing the bottom may be responsible in part. These questions, however, do not belong to this symposium.

Another geological problem connected with currents is that of the solution of lime and the elimination of organic matter in basins.

Solution is evidently moderate where *Globigerina* ooze collects in spite of adequate ventilation. It must be active in many lime-free clay areas because shells are certainly raining down onto the bottom. The high carbonate content of the sediments in the Sulu Sea forms a striking contrast with its absence in the deposits of the neighboring Celebes Sea at similar depths. The low oxygen content of the Sulu Sea bottom water indicates poor ventilation. But how is the ventilation in the Celebes Sea brought about and at what speed? I once ventured a primitive attempt at evaluating the available energy for flushing the deep basins of the Moluccas, by using an assumed rate of heat flow from the earth, tidal action, and the burning of oxygen to carbon dioxide, but obviously others could have done this more competently.

Similar questions arise concerning the organic matter in the sediments. Here emphasis is not only on its preservation or destruction but also as strongly on its production. This is a meeting point for physical, chemical, biological, and geological oceanology. The work on these questions carried out off California and certain theoretical studies of the shelf elsewhere are fine achievements, but those engaged in these questions will be the first to admit that no more than a start has been made. Because of the paramount importance to oil geology it should be possible to raise funds for further investigations.

The change from a recent deposit on the sea floor to a consolidated hard rock is a process involving, besides compression, mainly bacterial action and slow chemical reactions to pressure, heat, and groundwater flow. The chemical oceanographer is justified in delegating this subject to geochemists, but the alterations, especially of organic matter, start and even make good headway before the deposit is buried beyond the reach of a corer and while there is still active interchange with the sea water above it. Hence, it cannot be denied that there is a gradual passage from straightforward oceanological problem to true diagenesis (=consolidation to "rock") and even to rock metamorphism.

The products of chemical reactions taking place on the sea floor or in unconsolidated deposits are numerous and of great geological importance. Thus many ancient rocks contain phosphorite, glauconite, or pyrites and other iron compounds. Normally these are formed *in situ* or at least in the environment where they become buried. The behavior of silica is still little understood. It migrates in the recent sediment and part of the flint nodules of ancient limestones were evidently formed at an early stage. The precipitation of lime as calcite or aragonite in the shape of oolites or mud is a common phenomenon, but still insufficiently known. The change from calcium carbonate to dolomite has involved mighty building stones of the earth's crust. No wonder geologists are keenly interested in learning under what conditions these chemical processes take place. Precipitation appears to be limited to warm waters, but curiously enough the same can be said of solution in surface waters. This solution of limestone, especially of reef rock, has played a part in the coral reef problem. We still only suspect what the chemical and biological explanation is. We are still less certain as to the rate at which this solution takes place. Perhaps it can only model the surface, but the possibility exists that it acts swiftly and that all coral reefs were beheaded during the low levels of the Ice Age.

I have had occasion to point out that if this proves to be true a much more satisfactory explanation can be given of atolls and barriers. Darwin's upgrowth during subsidence evidently built the main part of the structure. But the present configuration probably results dominantly from postglacial growth on platforms produced by low-level solution in rain water and the surface film of tropical waters. For Darwin's theory fails to explain the usual combination of barrier with fringing reefs. Neither can it account for the almost total absence of passages through the reefs at depths greater than 100 m. These and other difficulties are accounted for by low-level beheading of the preglacial limestone mass.

This hypothesis is a modified form of Daly's glacial control that I call "decapitation." The advantages over Daly's views are that the very large atolls need not represent excessively wide erosion platforms and that coral growth need not have been suppressed to allow wave erosion. Hence, postglacial growth could start immediately on the outer rims and also in localities that receive few coral larvae. Daly's mechanical abrasion after killing of the corals would have left many stunted atolls and others with broad platforms 100 m deep outside the rim.

Differentiation of Epicontinental Environments

The type of sediment accumulating in a given locality depends on the two factors reviewed above, source and transportation. Without sources of sedimentary matter there can be no accumulation, and apart from sources *in situ*, there can be no supply without movement of the source materials toward their ultimate destination. However, the immediate surroundings also play a part in shaping the final product. Postdepositional solution of lime, decay of organic matter, reworking by waves, currents, or organisms, and desiccation may each have been active, but the environment and the two other factors are not entirely independent. The area in which a uniform type of sediment accumulates has a certain extent, often a large one, and therefore transportation must continue within the boundaries of the environment. In other words, there is transportation within the area itself. This may happen along the bottom, or the final lap of the transportation may be limited to vertical settling, e.g., for clay, windborne and volcanic dust, planktonic shells, and materials for *Faulschlamm*. In such cases, the absence of horizontal transportation along the bottom is a major condition producing that special type of environment. Some environments are closely linked with their source, for instance, deltas, tidal flats, beaches, reef lagoons, reef aprons, and glacial marine areas. Even more intimate is the link between source and sediment when the former is *in situ*, which is the case with organic reefs and shell beds, oolitic sands, and brackish swamps.

Given the fact that the two major factors in supplying the sediment are usually closely tied up with the nature of the "environment," the latter concept, taken in its broader sense, should constitute the most important element in determining what sediment is finally deposited. Looked at from this angle it may next be questioned what are the chief factors bringing about the differences between various environments. The answer to this must depend very much on what classification of environments is followed, and there is considerable danger of reasoning in a circle. If the classification of environments is based mainly on grain sizes, the transporting mechanisms are bound to come out on top in the quest for the chief determining factor. If based on animal remains, then living conditions would be the more important item.

I shall attempt to show that differentiation between environments by major topographic features is the most useful for epicontinental sediments because sources, transportation, and local conditions depend in large measure on the configuration of the crust. Topographic factors of importance are: depth, bottom slope, extent, topography of adjacent land and of the adjacent sea floor, degree of communication with the open sea, and connection with a source of freshwater. The principal nontopographic factor is climate (precipitation, evaporation, wind, temperature).

It would lead too far to discuss all these factors separately and in detail, but a few may be considered. Depth is of importance in that it governs the penetration of light and therefore influences plant growth and in that it limits the degree to which waves can act on the bottom and determines whether periodic emergence can occur. Slope is the main factor in slumping of bottom sediment and the setting off of turbidity currents. It also affects the action of waves and currents. Extent is significant because of its relation to the length of fetch for waves. Coasts will be subject to greater attack and the bottom will be churned up more intensively with increasing size.

Mountainous land, in contrast to low-lying country, will not only influence local climate, but will also deliver more and coarser sediments of local origin. On the other hand, there is less chance of the all-important influence of a large river mouth with its vast supply of fine sediment derived from a continent-wide area. The topography of the adjacent sea floor is in many cases of the utmost importance. Thus a neighboring basin can trap sediment and result in winnowing of its surroundings. The nondepositional edges of the continental shelf are large-scale examples of this. Sediments can be provided to a slope from nearby shallow water. Sliding and turbidity currents may carry them deeper. A depression, even in shallow water, is normally characterized by finer sediment and swifter accumulation than its surroundings.

The degree and depth of communication with the open sea determines salinity and temperature, and as exchange deteriorates, the influence of a dry or a humid climate increases. Likewise the barring of ocean swell and storm waves, not to speak of tsunamis, causes fundamental changes in the environment. Tidal range may be increased or suppressed by various degrees of isolation. The most obvious example is the sharp contrast in sedimentary conditions between inland seas like the Baltic or Hudson Bay, on the one hand, and the open shelves, on the other. The former collect all sediment carried in, whereas the shelves loose the bulk of the clay-sized sediment to the oceans. Partly enclosed seas like the North Sea and the Java Sea are intermediate because they are largely nondepositional.

The degree of ventilation of the bottom waters is a matter of great consequence to sediment formation. Solution of lime and decomposition of organic matter depend on ventilation. Its absence will result, in extreme cases, in suppression of benthonic life by anaerobic conditions, and iron sulfides and calcareous concretions may form in the sediment.

A final aspect of topographic influence on sedimentation is the amount of freshwater supply, a matter largely dependent on topography. Freshwater usually means that colloidal sediment and nutrients are furnished. Sand and even gravel may also be carried out to sea. In estuaries and fjords brackish conditions with a specific fauna can be induced. Anaerobic conditions are more likely to develop when surface waters are of low salinity.

A remarkable result of the meeting between freshwater and salt water is the establishment of various kinds of estuarine circulation with outgoing brackish and inflowing sea water. In some cases, such as the northern tributary of the Orinoco, this leads to the accumulation of clay within the estuary during the rainy season. The conditions happen to be such that removal in the dry season takes place because of the more powerful wave action at that time. In the Congo removal of sand appears to occur during river flooding. There are also other situations in which the clay accumulates as a dense cloud in the salt water wedge and awaits an exceptional river flow to flush it out to sea. There are many other interesting forms of mixing and of sediment distribution in river mouths.

The importance of climate to the formation of sediments is obvious. The strength, duration, and frequency of winds, and whether they are onshore or offshore are all-important to wave action. Winds may also cause upwelling and plankton bloom or the reverse. Temperature and evaporation likewise influence vertical circulation and the fertility of the water. Precipitation has its most marked influence, like most other climatic factors, in enclosed gulfs. All the climatic factors are of great significance to the biological environment and thus play a part in the production of shelly materials and particles of organic matter. One can hardly imagine greater contrasts than between the deposits of the sea floor off coral reefs, mangrove coasts, desert shores, temperate dune and rock coasts or arctic beaches.

In this review of environments several ecological factors have been mentioned. The remains of animals and plants enclosed in fossil sediments form, in fact, one of the most important sources of evidence on the environment of deposition, because organisms are very selective as to their conditions of life. Hence, ecological information, especially on organisms that have hard parts to fossilize, is of the utmost importance to geologists and, as we all know very well, ecologists and sedimentologists have already teamed up in many research projects.

Marine Geophysics

Some aspects of the biological, chemical, topographical, and hydrological influences on sedimentation have been reviewed, but the connections between marine geophysics and bottom deposits are no less close. A few items should be called to mind.

Seismic measurements of the thickness, stratification, and degree of consolidation are among the major sources of information for the sedimentologist. This is particularly true if the latter seeks to tie his subject to the problems of general geology and crustal development. Rates of sedimentation and nature of the foundation beyond the reach of coring instruments are matters of interest to the general geologist. Depth of rock channels and their fill are invaluable indications of lowered sea level during the Quaternary. It is hard to say whether echo sounding is straightforward geophysics, but we certainly owe a great improvement in our techniques to the geophysicists. The value of improved bottom charts for marine geology is obvious. The charting of subbottom surfaces by echo sounders of various kinds is proving useful in ascertaining rates of recent sedimentation and in finding water-covered land surfaces of the Pleistocene age, and other types of stratification.

Having noted how important the shapes of the solid crust are to the conditions under which sediments collect, the sedimentologist is bound to ask how these topographic forms are created and how they develop. The answer must be based mainly on geophysics.

Some inland seas, such as Hudson Bay and the Baltic, are closely linked with glacial isostasy, whereas others, such as the North Sea, Lake Maracaibo, Gulf of Paria, and the Persian Gulf, are surface expressions of ancient areas of subsidence. Deeper basins like the Mediterranean, the Black Sea, the Caspian Sea, and the Moluccan basins are of more Recent origin and must represent areas of very swift subsidence. The geophysical nature of the floors either oceanic or continental, the isostatic conditions, and the thickness of sedimentary cover are among the obvious urgent questions asked of the geophysicist.

Continental Terrace

A problem, not to say an enigma, of even wider scope is that of the origin of the continental terrace. This is the most ubiquitous and uniform of all major topographic shapes of the earth's crust, and yet the composition is fundamentally different in different areas. There are shelves that are most readily accounted for by erosion because there is so much rocky bottom close to the edge. Whether subaerial or marine erosion should be invoked and in what depths erosion has taken place, and how much time is required to produce the observed width are much debated questions that can be left to geologists to squabble over, but the geophysical investigation of the internal structure is an essential requirement. Marked tectonic activity of the coastal regions, both marine and terrestrial appears to characterize this type of terrace. Curiously enough such terraces are most usual along the borders of what many geologists, for disputable reasons, claim to be the most ancient ocean basin, namely the Pacific.

The opposite type of terrace is typical of the Atlantic, especially the eastern border of the Americas. There the probing geophysicist tells us he encounters a broad shelf underlaid by a thick column of sediment. The most probable structure appears to be a wedgelike thickening offshore with the strata outcropping on the slope, perhaps even bending up there. Available information is meager but it indicates a Mesozoic land surface sloping down to the floor of the ocean, and covered by a mass of sediment thickening seaward and then thinning again below the continental rise. Such a situation can hardly result as a primary accumulative form, even if we assume gradual subsidence progressing outwards in amount. A cutoff by a fault or by collapse, or erosion by turbidity currents are conceivable explanations between which a choice is as yet impossible. We do not even know whether the sediment collected on an open shelf or whether some shelter was provided.

A baffling problem must be pointed out. The terrace along the Atlantic border of the United States is among the largest in the world. Yet it was built in about 4% of geological time. In the remainder of the earth's history a number of such terraces must have been constructed in succession around the continents. There is no reason for postulating an exceptionally high rate of sedimentation off New England compared with other continental margins. Either those inferred and now missing ancient terraces have been incorporated in the high-standing continental blocks or they have been engulfed in the oceans. Both suggestions are unsatisfactory. Only a few continents have thick sedimentary prisms of sufficient magnitude along their margins to be considered in this light as former continental terraces. Moreover, in some cases the distribution of grain size denotes supply toward the continent; in others the thickness decreases on approaching the ocean edge from land.

Furthermore, if the continents had grown by sedimentation along their margins, one would expect to find deep-sea sediment at the base of the sedimentary structure. However, it is absent in ancient geosynclines. Finally, the continents are much too small to have been growing throughout geological time at the rate indicated by the present terrace.

If one were to postulate repeated terrace building followed by vertical collapse, that would require the assumption of so many revolutions for which there is no supporting evidence and against which geophysicists are bound to protest. Can it be, then, that the terraces are sapped from the outside by erosion, for instance by turbidity currents? This process would imply a huge volume of sediment carried to the ocean floor, more than anyone is prepared to admit as still lying there.

Turning to the Gulf Coast for enlightenment, we are confronted with a terrace of normal appearance. Here sedimentation has been even more spectacular in volume. Only modest, if any, gain in surface area for the continent has been attained at the cost of dumping shallow-water sediments to a thickness of 5000 m. Again only a few per cent of geological time is involved. A solution for this difficulty might be sought by pointing to the abnormally high average level of present continents. In the Paleozoic and Mesozoic, large sections were usually flooded by the sea. In the Tertiary gradual retreat of the oceans became more obvious, and at present the continents stand with their average level hundreds of meters above sea level. This must cause abnormal denudation and sedimentation, and in former ages the terraces may have grown much more slowly. This viewpoint is no great help, because all we can do is to reduce the number of times former terraces must have vanished from 25 to perhaps 5, but we cannot explain them all away.

The mystery is only aggravated by the fact that at several places along the borders of the continents geologists have found cogent evidence for land supplying vast amounts of sediment from outside the present continental margins. An attempt has been made to squeeze in a source in the shape of an island arc with volcanoes between the geosynclinal trough with sedimentary fill and the ocean, but the percentage of quartz sand in the geosynclinal troughs is uncomfortably high and that of volcanic ash unencouragingly low for this explanation. Neither does the small depth of deposition one must assume for most of the sediments recall the usual deep basins between the present island arcs and the Asiatic continent. There are some cases, like that of New Zealand, in which this suggestion of an island arc is no help, because it would have to be placed right in the deep ocean. Hence, I still consider the case a strong one for borderlands that have disappeared.

Perhaps it is time to explore a possibility that is contrary to the usual way of thinking. One must admit that there are several independent arguments pointing in the same direction that the deep-sea floor is a bottomless tub into which continental matter is ever disappearing. I see no compelling arguments for the popular notion that the continents have grown in the course of geological history, because to my knowledge old land surfaces are invariably found where the base of sedimentary prisms are exposed. All I am prepared to admit is possible growth of consolidated shields inside the borders of the continents. But a mountain range born from sediments deposited along but outside the continental blocks on the deep-sea floor still has to be found.

To substantiate the claim of insatiate oceans we have to consider, on the one hand, the inferred disappearance of former continental terraces and source areas of sedimentation, and, on the other hand, the absence of deep-ocean sediments on the continents (apart from Timor). Then there is geological evidence—to my mind unquestionable—that basins like the Mediterranean and the trenches of the Moluccas were produced by subsidence in the late Tertiary. Neither can one doubt the gradual subsidence of atoll foundations and uncrowned guyots. The submarine canyons off California with their partly rocky walls and the borderland topography of basins and ridges in that area strongly favour major subsidence of crustal blocks on the continental margin. Estimates of the thickness of oceanic sediment covering the deep-sea floor may not be very trustworthy. But the thickness measured seismically is so far below what one might expect, that it is tempting to assume transformation of sediment to a very dense rock induced from below. Finally biogeography and paleobiogeography can hardly do without transoceanic migration paths with more land and shallow water than is now present. Such isthmian or island-arc links have disappeared if they ever actually existed.

It cannot be claimed that any of these pieces of evidence is conclusive, but put together they at least suggest that we still lack insight into the nature of the contrast between ocean floor and continental block and do not know whether both or either are permanent. Geophysicists must assist in solving this riddle. They should help in deciding the question whether any of the ancient geosynclines accumulated their sediments on an open oceanic shelf or whether a closer parallel is to be found in inland seas, such as the Persian Gulf.

It is becoming more fashionable among geologists to admit the possibility of continental drift to account for transoceanic migrations. If the theory of Wegener is accepted the problem of continental terraces would have to be reviewed in this new light. Curiously, geophysics in the form of geomagnetic studies has provided the main impetus to this new trend of thought, whereas the stoutest opposition to continental drift has always come from geophysicists. Yet another recent suggestion is of an expanding earth. It is easy to raise objections to such bold speculations, but the bulk of the favorable evidence is sufficient to warn against offhand rejection of these ideas.

Marine Geology in Aid of Other Branches of Oceanology

An aspect more difficult to treat is how far other branches of oceanology can profit from geological investigations. Luckily the title of my paper does not oblige me to take it up, but to ignore it entirely would leave a serious gap in the discussion, so I will say a few words.

The sediments form the only permanent record in the oceans of what has happened in the past. One wants to know how far present current systems, chemistry of sea water, habitats of organisms, meteorological conditions, etc., are permanent and inherent to the conditions on earth, or whether they may have varied in position, or kind, and if so to what extent. Sediment cores are the chief source of information on this historical question.

The marine geologist can also attempt to act as intermediary between the field geologist examining ancient continental terraces and the geophysicist studying recent ones. A fine example of a well-exposed continental terrace with adjoining basin is probably that of the late Paleozoic of western Texas, although doubt has been expressed as to the validity of this comparison (J. E. Sanders, personal communication).

I put in a plea just now for more information on movements of water in contact with the bottom. However, this point can be reversed and sediments can be used as evidence to show what movements are taking place. In this connection it is worth pointing out that sediments tend to record either maximum velocities or average conditions for a locality, as the case may be, two values which can usually not be ascertained by current measurements. The occurrence of ripple marks, nondepositional conditions, sandy strata between muds, and winnowed oozes are examples. Marine chemists can learn from sediments whether lime is being dissolved or precipitated in certain localities.

Animal and plant remains in a sediment can give valuable information to biologists as to the limits of distribution and the abundance of species. The connection between nutrients, plankton blooms, the decay of organic matter, and sediments has been mentioned. In fact, whenever a marine geologist has a question for others to answer, he may be providing either data or at least food for thought to the one being interrogated. Personally I have found that attempting to answer a question is often more useful to the one who replies than to the inquirer, partly because the former is paying much better attention.

Accumulation of Clay in Tidal Flats

I want to treat in slightly greater detail a subject in which practically all marine sciences meet on common ground, that of the accumulation of fine material on tidal flats. This subject has received much attention in northwestern Europe, and recent advances made in Holland are worth recording.

The Dutch flats are situated between a row of islands and the shore of the mainland. There are watersheds that connect these islands with the coast. Here the ebb waters diverge and the watersheds are the first parts to emerge during ebb tide. Hence, each inlet supplies the tidal waters for the area between two watersheds. Each inlet has a major channel 20 to 50 m deep with strong currents and a coarse bottom cover of shells, pebbles, clay pebbles, and sand. This channel branches inward in all directions until small creeks are found which may run practically dry at low tide and reach close to the mainland coast and to watersheds. The bulk of the area is occupied by flats which fall dry at low tide. These are composed dominantly of sand, but certain areas are more muddy.

During the last centuries the land has been protected by dykes. Up against these the flats tend to collect fine sediment, and now and then new polders adjoining the land have been dyked in. Extensive mussel banks and a dense population of various shells living below the surface of the sand flats have an important function because they filter finely distributed suspended clay out of the water entering from the open sea and collect it in faecal and pseudofaecal pellets. These minute grains sink much more rapidly, and the result of the presence of the shells is that the clay can settle during slack water and tends to accumulate in the tidal flat area. Natural and artificial vegetation close to the shore enhances the accumulation ot sediment. Another form of coagulation is the production of floccules by chemical and biological influences. Compaction of clay beds, growth of algal films on the bottom, and reduction of wave action are three more factors promoting the accumulation of clay in the tidal flats.

If there were no other mechanism at work, the result would be to cause a higher clay content in the deposits than is found outside the row of islands. But once a certain stage had been reached, a balance should be struck between accumulation and dissipation. Ingoing and outgoing waters would contain an equal amount of suspended clay.

Two facts show that the situation is more complicated. One is that for long periods of the year a marked storage of mud may be seen to take place. The other is that the concentration of suspended clay in the water is much higher in the tidal flat area than in the open sea. This should cause diffusion of clay toward the outlets, in the same way as freshwater from the land soon disappears.

Less obvious mechanisms have now been discovered, which evidently play an important part in the storage of the clay. These have been termed "lag effects." As the water slackens towards the time of high tide its turbulence decreases and the clay pellets and floccules start to settle out. But before they have reached the bottom they have been carried inward a certain distance. As the average maximum current velocities decrease from the inlets to the mainland shore, the particle reaches the bottom at a point with lower current speeds than occur at the locality where it started to settle. Hence, the accelerating ebb current will not be able to pick it up when the same stage in the ebb tide has been reached at which the foregoing flood current started to drop the particle. The retreating tide will have to approach closer to its maximum velocity before the particle can be dislodged. Less of the ebb cycle can therefore be used for the outward journey, and the obvious result is that the particle cannot be carried back to the point from which it started its inward journey.

To this "settling lag effect" is added a "scour lag effect." This results from the fact that a stronger current is needed to dislodge a sediment particle from the bottom than is required to keep it in motion, once it has been set going. Then, the muddy suspension is spread out in a thin sheet at high tide, but is concentrated in deep gullies at low tide. This means that slowly settling particles can be deposited at high tide but not at low tide. This in turn renders the lag effects more efficient. Finally, the period of stagnant water lasts much longer at high tide than at low tide (Postma, personal communication). Hence, more lutum reaches the bottom and suffers scour lag.

Soon the combined results of these lag effects cause a particle to be carried so far inward that the ebb current cannot pick it up again. What happens is that with each tidal cycle the particle is transferred to a new mass of surrounding water that lies relatively farther from the inlet. There is a kind of diffusion away from the open water. This reasoning explains why there can be a much higher concentration of suspended mud in the tidal flat area than is found in the open sea, without loss of sediment taking place. In this respect freshwater added to the tidal water behaves quite differently because it cannot settle out. In a few tidal cycles it is dissipated and lost to the open sea.

The mechanisms described lead to a gradual decrease in medium diameter of the bottom sediment as one passes from the inlets toward the watersheds and coasts, and to a gradual accumulation of mud in the area. However, a different phenomenon occasions loss, namely the effect of storms. These churn up the mud, and the ebb current carries a large amount back to the sea. This happens on the largest scale when the storm drives exceptional quantities of water in at the windward inlets, across the watersheds, and flushes it out again through the leeward passages.

The general conditions do not change noticeably in the course of a few years so that roughly speaking the gradual accumulation and the spasmodic losses appear to balance each other. Whether there is secular storage or slow waste in the course of a number of years will depend on variations in supply, climate, changes of sea level, biological activity, and human intervention. Because of the huge amounts of sediment that have to be handled by the currents if they are to bring about a general rise or depression of the average bottom surface, many years must elapse before it is possible to recognize any tendency. The sense of any such tendency may be reversed before it has been possible to detect it.

This brief review of the storage of clay in tidal flat regions shows that it is evidently necessary to take into account animal and plant activities, physicochemical behavior of clay particles, tidal current systems, wave action, storm surges, laws of particle settling, compaction, suspension, measurement of grain size, and accurate charting. One even has to reckon with changes in climate and of sea level if quantitative assessments are envisaged.

In conclusion I should like to point out that the moral of this paper is obvious: oceanology is more than the sum of its component branches. We are members of a team.

V. Cycles of Organic and Inorganic Substances in the Ocean

Interrelationships between Aquatic Organisms Mediated by External Metabolites

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SEVERAL times since 1938 I have tried to review the progress made in this difficult field and feel all too incompetent to do so again in view of the number of those now working on one or another aspect of the subject. They now represent quite a formidable bibliography which provides a measure of the rate at which progress is being made.

Among those who anticipated the significance of such matters were Johnstone *et al.* (1924), Allee (1931), Bigelow (1931), Hardy (1935), and Russell (1936) and, however far we may yet have to go, their prevision has in one way or another already been amply justified. It was, in fact, owing to the inspiration provided by Sir Alister Hardy, when he was working on his theory of animal exclusion, that my interest was led toward what I called "non-predatory" relationships in ecology. I hope I may be forgiven if I try to look at some of the more recent progress in the light of these early thoughts. I do this the less reluctantly because of the comparative isolation in which the several workers on one aspect or another of this problem are still working. Yet this is essentially a field in which each worker needs to be in the closest touch with the findings—and above all with the thoughts—of all others working in it. We must therefore be particularly grateful to the organizers of this meeting, who have been successful in bringing together workers from Japan and Russia, from Canada and Scandinavia, from the United States and the United Kingdom, to exchange not only their results but their ideas.

In essence, the earlier thesis drew attention to the general tendency for all cells to release metabolites into the surrounding medium, both in relatively large (e.g., carbon dioxide) and relatively small (e.g., thyroxin) quantities, and to the vital roles which we have come to recognize that such processes play in the life of the individual organism. These roles range from the most subtle internal hormonal coordination to the means whereby the gametes are usually brought together. The latter are essentially external, but they initiate processes of development which are governed by series of chemical inductions. In each of these the release of metabolites by a cell or group of cells fundamentally changes the environment and modifies the reactions and development of neighboring cells, often at some distance in the body. The whole process is, or should be, a coordinated one, in which during evolution all the cells of the body have become adapted to the existence and metabolic processes of their neighbors. Indeed, it is when this coordination in one way or another breaks down that we consider a body to have become diseased, and this is particularly the case when, in tumerous growth, coordination is lost. Then cells, which should have been dependent and fitted into the general scheme, come to show a progressive "independence" of the specific metabolites which they formerly needed and which coordinated them (e.g., Klein and Klein, 1957). Death is the final independence.

The life of the normally organized "body" therefore shows us, at the one extreme, how the loss of internal chemical dependence leads to chaos and perhaps even death, while at the other those temporarily isolated parts of the body, the gametes, secrete into the external medium and are mutually influenced thereby.

Nor need one have in mind merely the gametes. In recent years the work of Raper (e.g., 1957) and others has shown how the sexuality of whole thalli of lower plants may be essentially under external "hormonal" control. In two heterothallic species of *Achlya* for example, no less than "seven distinct diffusible agents" take part in a chemical progression which is "a series of morphogenetically integrated stages in which each stage is initiated and quantitatively regulated by the secretion(s) of the last preceding stage" (Raper, 1957, p. 146). Somewhat similar interrelationships may be found between species. Whether superficially internal or demonstrably external, at all evolutionary levels, sex has been and is essentially an aquatic process, in which internal and/or external secretions play fundamental parts.

It was never debatable that, as in these instances, whole bodies secrete and excrete substances into their environment. Some of the processes were so familiar, however, as to hinder speculation in ecological terms, and particularly speculation on some common features of such processes. These releases of metabolites range from the familiar large-scale excreta, only some of whose ecological functions had been acknowledged, to the most minute quantities of a wide range of metabolic by-products (sex hormones and all the other familiar external secretions of plants and animals, from scent and sweat to mucus, etc.). There appears, however, to have been little or no realization of the general implications that, after release of such metabolites *all* become part of the environment of the neighbors of that organism, as indeed do the decaying products of the whole body after its death, and that organisms throughout evolution have been exposed to such a changing organic milieu. While some of the more obvious ecological roles of the grosser metabolites were appreciated, it was not until the ecology of the microorganisms had developed sufficiently that a wider historical picture could be dimly anticipated.

It must have been aspects of this picture that the more thoughtful marine biologists of the twenties had in their minds, perhaps particularly Johnstone *et al.* (1924) with their "group symbioses on the great scale." For this is what some of us now feel entitled to expect; in isolated instances the basic evidence for their existence is now available. It lies not only in the steadily increasing evidence concerning the large quantities and the particular nature of the innumerable organic substances to be found in aquatic media, but also in the certain knowledge that they are secreted, excreted, or are otherwise derived from living organisms. Further, we now know that many organisms can live and grow only if supplied with organic substances which others are known to produce. Vitamin B_{12} or one of its analogues (e.g., Provasoli, 1958; Southcott and Tarr, 1957) is at present the best known of these, but others (thiamin, niacin, steroids, organic acids, etc.) are known and others are being found (e.g., Provasoli, 1958; Vishniac, 1955; also various contributors to the afternoon sessions of this Congress). A recent development is the demonstration by Dr. Bentley, at Aberdeen, that potent substances resembling the growth hormones of higher plants are produced by planktonic and other algae and even by zooplankton, and are released into the medium (Bentley, 1958; 1959). There are results, too, which demonstrate that some free metabolites may be harmful to other members of the community while, as was foreseen, there are hints that sometimes the same metabolite may be harmful to some and necessary, or at least beneficial, to others. This may be one aspect of the evidence that there has been adaptation to optimum concentrations of the metabolite in question. Meanwhile, in his paper, Professor Friedrich (p. 257) gave us food for thought in his reference to the photosensitizing possibilities of many of the fluorescent substances present in the sea.

Just a moment's thought about the wide range of substances (from carbon dioxide to B_{12}) with which we can be concerned (e.g., Vallentyne, 1957) suggests the need for some classification. In my enthusiasm for the general thesis, I was all too negligent about this previously, and proper attention cannot be given to it here. Meanwhile, I will roughly distinguish, for future analysis, (*a*) substances such as the grosser products of decay and excretion (amino acids, carbohydrates, etc.), perhaps together forming the bulk of organic compounds in the sea; (*b*) those more diffuse substances such as carbon dioxide and oxygen which are still very appreciable and, moreover, are metabolites exerting immediate and vital effects on other organisms in the community; and (*c*) those which, broadly speaking, are measurable in terms of parts per million or even less. The last in turn, for the present, may be divided into (*a*) known and potent metabolites within the body, such as B_{12}, which may be expected (and in some cases shown) to play similar parts within the community—perhaps the term ectocrines is best restricted to these—and (*b*) less known substances with which members of the community may have developed ecological links or sensitivities. Alternatively, there is the possibility of a functional classification, loosely divisible into (*a*) "nutrient" substances, (*b*) "growth" substances, and (*c*) "behavior-stimulating" substances.*

However this may prove to be, the witches' brew which the seas comprise, and the evidence we are slowly obtaining provides the necessary basis for mediating some of those features of marine ecology which had previously been puzzling: some aspects of the initiation of the spring outburst, of the flowerings which occur at water boundaries and above all of "succession" itself. Here, too, we can be sure lies at least a part of the explanation of the facts which led Hardy (1935) to postulate his theory of animal exclusion. The metabolism, and ultimately death, of one organism is always modifying the environment of another. If that modification is appreciable, the others must either be tolerant or must adapt themselves in order to succeed. Some organisms appear to be susceptible and must have an avoiding reaction or fail; others appear to have evolved a significant deficiency which certain neighbors can supply—doubtless attaining increased efficiency elsewhere in their own metabolism at the cost of an increased dependence! Some benefit without that necessity; others may be merely tolerant, although over the generations mere tolerance is unlikely. In one way or another, these "dependencies" give at least an appearance of integration in the community. It is not the close integration which characterizes the organized body, nor is it just the product of the inorganic environment. It is a loose but organic integration. In some respects its extreme developments may be found in true symbiosis and parasitism. Given the facts, evolution could be expected to bring about such relationships, including reciprocal relationships, some of which would indeed be "group symbioses on the large scale."

Since 1938, and particularly since 1947, several of these possibilities have been confirmed as facts, chiefly by experiment.†

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* A very interesting discussion of interrelationships and terminology in this and bordering fields is given by Karlson and Lüscher (1959).

† While only representative, reference may be made to the various papers listed by Lucas, (1938, 1947, 1949, 1955, and 1958), references here will mainly be selected from papers published recently; relevant bibliographies are given by Provasoli (1958), Hutner *et al.* (1958), and Saunders (1957), as well as in papers contributed to the afternoon sessions of this Congress.

Almost before they were made, however, such experiments were liable to several kinds of criticism (e.g., Talling, 1957). Even though a relationship might be established *in vitro*, do the same conditions ever, or reasonably frequently, hold in nature? Even though a substance is demonstrably produced, will it not rapidly be modified in nature? Even though organisms may have demonstrable metabolic requirements, such as for B_{12}, are these metabolites ever scarce enough in nature to be significantly limiting? Alternatively, does the hypothesis postulate so many variables that we can never hope to disentangle them? Again, criticisms have been raised that some of the effects demonstrated or postulated are not typical of the normal, active life of the organism mediating them but only of its decay. This is perhaps the simplest to refute, since all organisms are subject to decay. Ecologically speaking the stage at which the metabolites are produced is less relevant. What is significant is that following their decay other and specific organisms "succeed," sometimes literally amidst the fruits of that decay.

The other criticisms are more serious, if only because they are more difficult to answer by experiment and observation. Information we have to date about B_{12} in nature provides a good example. Among others, Cowey (1956) demonstrated (with samples collected by Dr. Johnston from our research vessels) that an annual cycle of B_{12} content might be presumed, and Droop (1957), to whom we owe so much in this particular field, was led to suggest that so slight were the phytoplankton requirements in terms of B_{12} that, even at Cowey's lowest values, there might always be ample supplies for the greatest concentrations recorded. In reply, Daisley (1957) made the sound point that Droop had allowed only for the standing crop and not for overall production. Further, adequate allowance cannot as yet be made for the relevant parts played by free B_{12} and bound B_{12} in this argument (Daisley, 1959) although we are acquiring many clues as to the various needs for B_{12} and its analogs and as to substitutions for these (Droop *et al.*, 1959). We are as yet some way from a final answer, but we do know that B_{12} is produced and its availability varies, while many plankton algae either need it or can benefit from it (e.g., Provasoli, 1958).

As to the suggestion that the hypothesis visualizes too many potent influences, they are not likely to be equipotent; as in the body some will prove of major potency and others significant but relatively minor. It is the first two criticisms which are the most cogent, although to some extent the points just made for B_{12} are relevant to the first—as to whether significant quantities are found in nature to meet the postulated needs—just as the known facts about the harmful effects of certain dinoflagellate toxins in nature are relevant. As to the suggestion that some undoubtedly potent metabolites might speedily be changed chemically after release, in so far as our increasing knowledge only serves to confirm the idea of the sea as a veritable witches' brew, so it may well be! The secondary product, however, may be no less significant. These criticisms are, in fact, more relevant to the difficulties of imitating *in vitro* the conditions *in vivo*. Experiment classically demands the simplicity of a minimum number of variables, for example, bacteria-free algae, while in nature communities are usually complex, and a bacteria-free diatom probably does not exist! At present, even when we have valuable hints from the laboratory, all too often we are entitled to conclude only that those or related processes may occur in nature sometimes and somewhat, and the vital questions remain as to how often and how much. We have only to think for a moment of the enormous labor involved in answering some of these questions, even when we have evolved all the necessary assay processes, to see how essential it is to select carefully the most useful processes for investigation. If, therefore, we are reasonably convinced of the value of such work it may be useful to review possible lines of investigation.

1. From many points of view, the culture of microorganisms comes first. It is from the early attempts to grow plankton algae, so ably followed by workers such as Provasoli and Droop, that some of our best clues have come, and others will follow. Even in this best investigated field there is still much to be done in evolving precise culture media for algae, and particularly for some of the more or less oceanic diatoms and dinoflagellates which have so tempted us and defeated us in the past. Some clues in this field

have been obtained by my colleague Dr. Johnston (1959), by the use of antimetabolites, as to the metabolic requirements of several species. To me, it has always seemed that one approach to this problem lies in the use as media of filtrates of organisms known to grow earlier in the succession, and more might be done in this manner. Any successes could be followed by rigorous chemical analysis or bioassay. That, however, is merely a suggestion. What is certain is that work of these kinds is fundamental to most of the other lines of investigation. In conjunction goes an urgent need for more work in the field of marine bacteriology (and mycology, for example, see Vishniac, 1956), and in the effects on bacteria of algal (or fungal) metabolites, and *vice versa*.

2. Then, or rather in association, there is the essential work in the field—what is significant and the vital questions of how often and how much. We are only just beginning on this task at the ectocrine level (e.g., Wilson, 1958; Johnston, 1955; Cowey, 1956; also various contributors to the afternoon sessions of this Congress), and know little enough at the nutrient level! It will require very careful selection of projects if progress is to be made economically, and standardizing of methods between workers and countries (e.g., Daisley, 1959). Doubtless some of the laboratory results will prove to be illusory or irrelevant, and others less important *in vivo* than they can be *in vitro*. This possibility exists even for B_{12} (e.g., Droop, 1957; Vishniac and Riley, 1959), but there is no doubt that relevant evidence will be found. As an example, I may mention another part-time investigation by Dr. Johnston. From a number of cruises he has obtained groups of sea water samples, for special filtration and standard nutrient additions, so that their essential differences should lie as far as possible only in their dissolved organic contents. When used as media for subculture of laboratory algae (cf. Johnston, 1955), differential growths were obtained, and this alone will not be surprising. But, although his results are still only interim and cannot as yet be said to be reproducible, the interesting thing is that for a few routine cruises these differential results grouped themselves into suggestive spatial patterns, and not at random.

3. In particular, by its very nature, such work leads logically to progress in the tantalising field of ecological success and succession, obviously in the phytoplankton and perhaps also in the

zooplankton. We have one clue here in the observations by Marshall and Orr (1952) that successful spawning of some copepods is closely dependent upon local phytoplankton growth, but it will be important to know what degree of specificity this entails, among other things.

More widely ranging is Hardy's (1935) theory of animal exclusion, which stimulated so much of the valuable work that has been done in the last twenty years. Although doubtless some of the phenomena which he collected together under this head may now be seen as instances of general ecological or predatory balance (Harvey, 1934; Beklemishev, 1957; Bainbridge, 1953), others are less easily explained away. Indeed, if we view Hardy's thesis in the terms of what we now know of the production cycle of many algae, it would be surprising if some zooplankton organisms were not adversely affected by the by-products of the later stages of an algal flowering, quite apart from the diffused products of the "log" phases of at least some of them (e.g., *Prymnesium* and *Gymnodinium*). Among more recent work relevant to Hardy's theory is that of Ryther (1954) on the effects of algal products on the filtration rate of *Daphnia* and also that of Sieburth and Burkholder (1959), which so remarkably links the antibacterial activity of some Antarctic algae, via their euphausian predators, with an apparent bacterial sterility of a euphausian predator, the penguin *Pygoscelis* and other Antarctic birds.

4. Space and time are intimately related in ecology, and some of Hardy's examples were undoubtedly aspects of exclusion in time, or "succession." Among others, reference must be made to the interesting observations and ideas set out by Margalef (1958), regarding heterogeneity and the parts played by ectocrines, particularly in the later phases of succession. His view that "most instances of biotic heterogeneity are cases of successional heterochrony" is most stimulating. Similarly, the basic investigations of (1) and (2) above may be expected to lead to better understanding of boundary problems in pelagic ecology, yet another spatial aspect of succession, and of the initiation of phytoplankton outbursts as well as of phenomena of special interest such as red tides.

5. If, at first sight, the processes of succession seem somewhat

academic, only a moment's thought is needed to appreciate their relevance to fertility, for example. In the past this has been regarded in terms of basic nutrients, water movements, etc., but there are good reasons now for taking into consideration also the available metabolites: first, because (in some instances at least) we know that phosphates and nitrates alone may be insufficient, but even more because in many important respects fertility alone —overall production, indeed—may be irrelevant, however great. I have touched previously (1956) on this aspect, which assumes greater importance as we learn more about the nutritional needs of particular organisms and their tendencies to select some foods and/or avoid others. Rich phytoplankton production alone does not govern the successful growth and spat-fall of oysters, but rather the production of a very small number of specific algae on which alone the oysters can thrive (e.g., Davis and Guillard, 1958): these in turn may depend on specific chemical requirements being met (e.g., Hutner *et al.* 1958; McLaughlin, 1958), or particular harmful ectocrines not reaching dangerous concentrations (Davis and Guillard, 1958; Loosanoff, in discussion of Wilson, 1958, p. 99). To the oyster, all the other species are weeds! Plaice production again does not depend merely on the gross success of local invertebrates but rather, at a critical postlarval phase, on the availability of a few, perhaps only one or two, zooplankton species (Shelbourne, 1957). We can now expect these in turn to have their specific needs! Yet another example is provided by the work of Shivaishi and Provasoli (1959) on the factors required for the growth of *Tigriopus japonicus*. As my colleague, Mr. Steele, has so rightly said (1958), emphasis on measuring the grosser aspects of productivity has tended to distract attention from specific composition. Yet, species selection is as fundamental a process in contemporary ecology as in that large-scale ecology which is evolution itself. Indeed, along with the evolution (in both senses) of free metabolites has proceeded the evolution of new ecological niches and links—and often enough their occupation must have created yet further possibilities of evolution. Doubtless nowhere is this more evident than in aquatic media, as Waterman (1958, p. 348, commenting on Margalef) has pointed out.

6. Nor can such processes be neglected in attempts to increase production by artificial increase of nutrients. At the lowest level, free metabolites may be concerned in securing the maximum sustainable basic production. As in (5), however, they are even more likely to be relevant to any specific objectives for which fertility is being increased, directly or indirectly. By contrast, as has already been found in the carp culture of Palestine, free metabolites (e.g., of *Prymnesium parvum*) can also be extremely harmful, and the simple destruction of the "pest" may not necessarily be the most efficient cure, ecologically speaking.

7. Perhaps to a lesser degree, ectocrine processes may also be relevant in any attempts which may yet be made to culture "food" algae on a commercial scale (e.g., Burlew, 1953). However this may be, and there are serious problems to be faced before it becomes a reality, there still remain possibilities of algae being cultured for the extraction of their metabolites, if one can judge by the interest some of those few ectocrines already isolated have attracted in the medical world (e.g., Schwimmer and Schwimmer, 1955; Hutner *et al.*, 1958).

8. These, then, are a few of the reasons why intensive but selective work in this field is likely to be reasonably profitable. In these hunches, however, I have been concerned chiefly with those metabolites which perhaps best deserve the term "ectocrines," and which are effective at concentrations of the order of 10^{-6} to 10^{-8}. Yet they are only a minute fraction of the metabolites released by aquatic organisms. We now know that, apart from oxygen, normal algal metabolism can involve the release of relatively very large amounts of carbohydrates, etc., even up to 50% of production (Allen, 1956; Lewin, 1956; Fogg, 1958; Guillard and Wangersky, 1958). These amounts, along with proteins, etc., may be increased when an algal flowering decays and when animals excrete and die. Krause (1959) has shown how rapid may be the breakdown of dead zooplankton, up to one-third of the whole being lost to the environment within a few hours and one-half within a day. It is not, therefore, surprising that the total quantities of organic matter in solution in natural waters may frequently be very large, often exceeding several-fold the total

quantity of organic matter in living form in shallow waters, and exceeding it very much more overall throughout the deeper parts of the ocean; their ecological significance is likely to be no less. Indeed, both Collier (1958) and Provasoli (1958) have drawn attention to the role the massive amounts of some organics may play in maintaining those ectocrine-producing bacteria which are so essential to the life of other microorganisms—once again "group symbioses on the large scale." We know also that some at least of the smaller molecules (amino acids, etc.) can be used directly as nutrients by many plankton algae,* thereby short-cutting the ecological cycle, and a reference here may not be inappropriate to the microorganisms of the layers beneath the photosynthetic zone itself. In recent years we have had several hints that significant elements of production may proceed in deeper layers [or under ice (Rodhe, 1955)], perhaps ultimately dependent on the activities proceeding above, but directly the result of microorganic activity in the absence of light, in the muds and in the deeper layers of the ocean. The late Dr. Fabius Gross gave me the first hint of this, and Ferguson Wood (1958) has recently given another, with his evidence of heterotrophic diatoms in the deep community (further hints are given by Lewin and Lewin, 1959). Quite apart from their functions in the depths, sooner or later the products of such activity come to the surface in upwellings, etc.; useful work might well include careful investigation of the physiological qualities of waters from some of the classical areas of upwelling.

9. Meanwhile, despite Krogh's (1931) masterly disposal of Pütter's (1908) rash claims, the possibility that some dissolved organic matter in relatively gross amounts may yet be shown to provide nutriment for aquatic animals cannot now so easily be dismissed (Morris, 1955). At its grosser level, this possibility is more analogous to the relationships between parasite and host rather than to the coordinated hormonal interrelationships of the body cells. Parasites, harmful and tolerated, live among and on

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* A fascinating new aspect of this is shown by Smith *et al.* (1959) in their work on the possible preference by some algae for complexed carbon dioxide as a carbon source and the role this may play in photosynthesis, etc.

the internal metabolites of their hosts. Can we now be quite sure that some at least of the marine metazoa, particularly in their youngest stages, are incapable of maintaining themselves in similar ways, wholly or in part?

10. May I now mention one or two examples of aspects of the behavior of marine organisms which are now only just beginning to be understood? First, following the early observations of Nelson on the pumping reactions of the oyster, Allison and Cole (1935) demonstrated a relationship between the feeding reactions of the barnacle and the local phytoplankton abundance, while Collier *et al.* (1953) further demonstrated a specific pumping reaction in the oyster to the variable free carbohydrate content of the water.

Again, Davenport and Norris (1958) have just shown how the small fish *Amphipyron*, apparently via a mucus secretion, influences the anemone *Stoichthys* so that gradually a state of tolerance is set whereby the fish can come to live among the tentacles of the anemone without harm and possibly with benefit. A fundamental behavior reaction toward fish and other animals in general is thus regularly changed via an ectocrine process when members of these two species come together. Other examples of this type of ecological modification of behavior are sure to be found.

My next example concerns the apparent homing responses of some fishes to free organic substances derived and carried by currents from their "homes," to which they presumably became conditioned during early life (Hasler, 1954). Here we may also have a clue to the problem of the more generalized "homing" of so many sea fish, whereby the annual drift of their planktonic eggs and larvae away from the spawning centers has to be counterbalanced by the annual return of the adults to spawn in approximately the same places. This is not to suggest that these important movements are governed only in such ways. Yet, whatever parts they may play, response to postulated orientations by natural light or geographical "memories" still seem inadequate to account for some of the homing reactions which observations seem to demand.

This last may seem to be the most speculative of all and yet, as modern human beings, we are perhaps particularly ill equipped to appreciate the part played by smell (or taste?) in the lives of most animals. Another very relevant example is the observed avoiding reaction of Pacific salmon to the extracts of mammalian skin at concentrations of only 1×10^{-7} or less (Alderdyce *et al.*, 1954). Even though "ectocrine" may not be the most suitable word with which to label such processes, they do appear to come within the category of reactions mediated by external metabolites.

These, then, are a few of the lines along which useful progress may be made. They are not likely to prove the best, for each year we get fresh clues. Each presupposes the adaptation of organisms to the environmental modifications produced by the free metabolites of others, whether on the large or the small scale, which I came to view as a key feature of ecology, as of evolution itself, and a feature of terrestrial ecology in some respects no less than aquatic ecology. And here, perhaps, I may beg to differ from Dr. Buzzatti Traverso (1958, p. 619) in the remarks which followed his very kind reference to my ideas when concluding the conference on "Perspectives in Marine Biology" at La Jolla in 1956. Then he said "It may perhaps turn out that the main difference between marine and terrestrial living form lies in the requirement by the former of metabolites." But, at least at the microlevel, examples of such dependence can also be found on land (e.g., sex processes, for which microaquatic niches of one kind or another have been maintained or adapted, and, in the free air, smells mediating essential processes or habits). Nor must we forget the large-scale instances of ecological organization mediated by the release of metabolic by-products such as oxygen and carbon dioxide. They "condition" the existence of life on earth and must have conditioned its evolution, on land as well as in water (see, for example, Nursall, 1959).

If this talk serves no other purpose, it may of itself perhaps serve as a practical demonstration of one last aspect of the thesis with which I have been and am concerned: that the release of metabolites has been an important factor in mediating interrelationships within the community. In this special instance, the excretion of "waste" carbon dioxide by a higher animal while breathing has become adapted, and very specialized auditory and mental processes have evolved with it, as the principal means of human communication. As a faculty it is often abused, and not least in this present age, but there are those who have seen in speech and its derivatives, the highest achievements of man. Through it and its more recent evolution as the written word most of human ecology today is organized—and sometimes disorganized. As free metabolites, both carbon dioxide and oxygen, on land and in the water, illustrate "group symbiosis on the great scale" and, if for no other reason, this might have encouraged us earlier to look for the more subtle examples, such as we are now finding.

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Primary Production

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ONE difficulty in preparing this paper has been that I feel there is really no subject that can properly be called "primary production." Rather, the phrase is used as a focus for many diverse interests connected with what may be called, rather vaguely, the relation between phytoplankton and their environment. The interest in this field is not merely to measure production but to try and explain how these values arise, not only from the physiology of the plants themselves but also from their interaction with the physical conditions and with the animals that graze on them.

The basic problem in relating these various trophic levels is the great complexity in the species composition of the plants and animals. The one feature of primary production which perhaps separates it from other branches of marine biology is its attempt to escape from this complexity by considering plants and animals as chemical rather than biological entities. Thus the common unit is quantity of organic carbon and, for example, grazing on the plants is expressed as the rate at which plant carbon is eaten by animal carbon.

This hypothseis of simplicity is a much blunter instrument than Occam's razor, and it is obvious that too much has been cut away. In using the same example, salps and copepods can hardly be expected to have the same feeding rates for each unit of their carbon content. Beyond this there are the problems raised by Lucas (p. 499), problems of the effects of traces of organic substances on particular species and on the interrelations between species. In ignoring these problems, we are postulating that these "metabolites" may determine which species compose the population but that the total population is determined by the much simpler large-scale factors we study. Thus this hypothesis of simplicity must be regarded as a first approximation of unknown extent, and a main present purpose of laboratory experiment and sea sampling must be to find out how and where it breaks down.

As I have said, this apparent simplicity is imposed by the methods of sampling. Plant pigments, especially chlorophyll *a*, are measured by the methods of Richards (1952) and others. The chlorophyll values are obviously related to the rate of growth of the plants as well as being an index of the amount of plant carbon present. The ratio of certain of the pigments may also provide an indication of the physiological state of the plants, particularly with respect to nitrate deficiency (Yentsch and Vaccaro, 1958). But certainly one of the most important of the new methods is that introduced by Steemann Nielsen (1952), which provides a measure of production by using radioactive carbon. Its widespread use was described in a symposium held by the International Council for the Exploration of the Sea at Bergen in 1957.

Yet these methods raise many problems since their interpretation is often not so exact as the measurements themselves. Thus the conversion from a pigment measurement to an estimate of plant biomass in terms of organic carbon has very wide limits since both high light intensities and low nutrient concentrations tend to decrease the chlorophyll to carbon ratio. In particular there is a daily periodicity in photosynthesis (Doty and Oguri, 1957) which in the tropics can amount to a factor of five between the morning maximum and afternoon minimum. This periodicity seems to correspond to diurnal changes in chlorophyll content (Yentsch and Ryther, 1957; Shimada, 1958).

The principal discussion, however, has been over the interpretation of C^{14} values. This C^{14} method is important because it is at the focus of the diverse interests I have mentioned, and so the interpretation of its results involves knowledge of many of the factors affecting plant growth. Because of its sensitivity, it has revealed previously unconsidered complexities in these relations. The original argument, whether the method measured gross or net production, that is, whether it measured photosynthesis or photosynthesis less respiration, has led to questions and experiments about the effects of light inhibition, the mode of nutrient limitation, and, especially, the effect of respired carbon. For the last of these, Steemann Nielsen (1955) and Ryther (1956) in rather similar experiments but with different organisms reached different conclusions. Ryther's results imply that somewhere within the respiratory cycle all the respired carbon is reassimilated by phytosynthesis, while Steemann-Nielsen found an interaction amounting to only 50 to 70% of the respiratory rate. Because of such possible disagreement it may be that the correct interpretation of C^{14} values will not be expressible in one simple formula as we had hoped.

Another example of the type of complexities which have arisen comes from the data on nutrients. In addition to phosphate, nitrate and silicate are now measured regularly (Mullin and Riley, 1955; Armstrong, 1951), and variations in the relative proportions of these nutrients are found to be more widespread than had perhaps been thought (Ketchum *et al.*, 1958). This makes it more difficult to think in terms of a single index for the effects of nutrient deficiency on a plant population, yet this index has been one of the main features of the early hypothetical systems to explain plant changes (Steele, 1959).

However, the most difficult sampling problem is probably that raised by the zooplankton. With the plants, filtered water samples catch effectively all the organisms, and chlorophyll extraction measures a common factor which is directly connected with their growth. For animals the displacement volume, or the dry weight, of net hauls has been used to provide single values which can be converted to carbon content for comparison. But no single mesh size or speed of hauling of a net can catch all the animals, nor do the values obtained differentiate between herbivores and carnivores. Thus the figures are rather poor indices of the possible effects of grazing on the phytoplankton and this is one of the main factors we need to know. This inadequacy is perhaps the main difficulty in sampling for quantitative information about production cycles.

Apart from the C^{14} technique there are three other main methods that have been used to estimate production.

One of the first methods (Gaarder and Gran, 1927) was to find the oxygen produced by photosynthesis as the difference between the oxygen concentrations in a bottle exposed to the light and one kept in the dark. Since this method is not very sensitive and since it now appears that errors occur when sea water is kept in a bottle for any length of time, it is confined to occasions where the productive rate is fairly high, and significant results can be obtained in experiment of, say, less than 12 hours. For this reason it is not possible to use this technique to get values of gross production in those areas which are of especial theoretical interest where production is apparently low because of nutrient limitation.

The other methods are less direct than the C^{14} or the oxygen technique. The rate of photosynthesis can be calculated from chlorophyll, light and transparency data, assuming a general relation between light and photosynthetic rate derived from laboratory experiments (Ryther and Yentsch, 1957). This is probably the simplest and best method of getting an estimate of the gross production; the problem is that since the net production is of most interest, a value for respiration is required, and this raises the difficulties already mentioned. The net production can be calculated from the rate of disappearance of a nutrient, usually phosphate, from the water. This method, however, does not allow for the rate at which phosphate is accumulating in the euphotic zone owing to the breakdown of organic wastes, and this rate of breakdown is still comparatively unknown and may be very variable (Cushing, 1959a).

In general, then, the problems of interpreting any one measurement depend on the other factors being measured, and a main result of this is to emphasize that in the sea no single sampling method is sufficient to portray primary production. On the other hand, the common properties of these techniques, the comparatively large number of observations that can be made, and the use of carbon as a common unit enable easy comparison between different areas and times. In this way it has been possible to go to any part of the ocean and estimate a range of common parameters relevant to plant production. This ability to compare directly areas with very different species composition has been the greatest single advantage of these methods. Such descriptions of a wide variety of environments have in general supported the earlier ideas of Harvey (1942) and others showing that where there is a good supply of nutrients to the upper waters there is high plant production leading to good zooplankton crops; and that where nutrients are low, the reverse is true. Quantitative models of these relationships have been fairly successful (e.g., Riley *et al.*, 1949) suggesting that the interdependence is in fact comparatively simple (Steele, 1959). However, there are occasions when the results do not quite fit these patterns. It often happens that, although the broad general picture just described may be satisfied, when the details of the data are studied, many anomalies appear.

Because the general ideas seem fairly well established, the emphasis is now turning more toward detailed attempts to show quantitatively how causal relations operate in particular situations. The papers at this meeting have provided examples of this. Riley (1959) has shown the significant roles of low respiratory rate of the plants and low grazing rate of animals in permitting a winter outburst in Long Island Sound. Menzel and Ryther (1959) show, by a detailed series of samples in the Sargasso Sea, that the production is not necessarily at the constant low value that has sometimes been supposed. Cushing suggested, as Beklemishev (1957) has also done, that the food supply of the bottom fauna may depend on the inability of the zooplankton to assimilate the available plants during short periods of high production, thus allowing organic matter to sink to the bottom. In this way the bottom fauna would depend for their food throughout the year, not on the total yearly production but rather on the size of the production peaks. These examples are all cases where events during a quite short space of time may dominate the yearly picture, so that detailed sampling is necessary to reveal them. They also show how values are needed for what may be called the "biological constants." Some of these have been mentioned, such as the respiratory rate of plants or the relation between light and photosynthesis. Others are the sinking rate of plants, the effects of low nutrient concentrations, and the grazing rate of the animals. All these have been studied in the laboratory but because of the unavoidable artificialities of laboratory experiments, the experimental results cannot always be applied straightforwardly to observations in the sea. An example of this is that it is very easy to demonstrate the slowing down of plant growth due to nutrient deficiency in a culture flask, but this effect has not yet been observed directly in the sea (except for some recent preliminary results by Dr. Ryther). Again, the experimentally determined filtering rates of zooplankton show a wide range of values (Cushing, 1958) which may be due to variations in experimental technique (Cushing, 1959b). Thus it is necessary to check the values by seeing if, in their natural environment, the filtering rates will provide the animals with sufficient food to meet their respiratory needs (Conover, 1956).

In this way difficulties arise in comparing the simple and logical structure of an experiment with the often apparently chaotic sequences of data from the sea. This may lead to a certain divergence between the two approaches with the laboratory experiments regarded as the source of hypotheses and the observations giving merely a broad descriptive indication of the probable consequences. But because of the difficulties inherent in the methods of sampling and in the laboratory experiments, no hypothesis is really acceptable until there is good evidence for the particular causal relations operating in the sea.

Once more, then, from this point of view there is the need to devise programs which will provide data to test critically particular hypotheses. At the same time such detailed studies can provide ideas about possible features of plant behavior which might not be expected either from broad surveys or from work with cultures. The general problem in finding a way to analyze such data is that no particular feature can really be separated from the rest, and one has to consider several possible interrelations at the same time. I should like to illustrate now some of the complications that arise in a detailed study of observations by using a theoretical model of the production cycle which I developed for the North Sea (Steele, 1958). To construct it I used estimates of photosynthesis, respiration, grazing rates, and so on, all of which, as I have said, are rather dubious, so that the model demonstrates what the questions are rather than providing answers.

The smooth curves in Fig. 1 represent the idealized sequence of events in the euphotic zone for temperate waters on the continental shelf where there is moderate vertical mixing. If the points on these graphs are considered as sets of data, collected perhaps on a cruise over the area, then using the usual methods of presentation, I have in Fig. 2 graphed plants against phosphate and animals against plants, with the arrows showing the direction of change with time. For the former it is obvious that the curve does not follow any simple relation. For the latter, however, the relationship is more subtle since a correlation exists, as suggested by the dotted line. With a sufficient scatter of values, the roughly elliptical form would not be obvious. The rather poor correlation would not be due to the inadequacy of the data but it is inherent in the relations involved in the time lag between plant and animal growth. This example has been derived from time changes, but

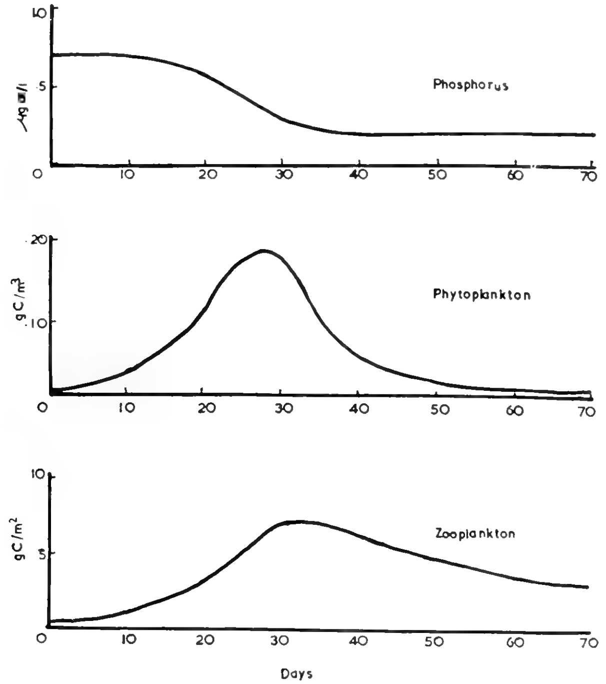


Fig. 1. Theoretically computed changes during a spring plankton outburst.

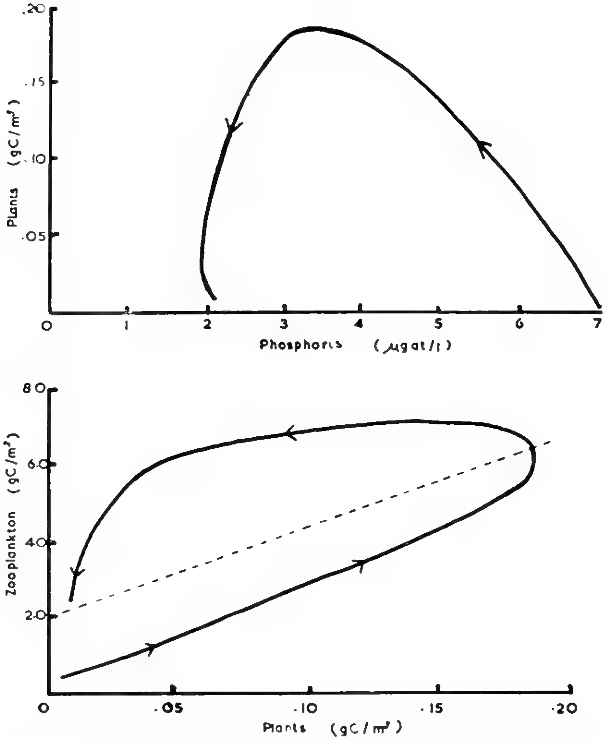


Fig. 2. Theoretically derived relations between phosphate-phosphorus, plants, and zooplankton.

from discussion with Mr. Holmes of the Scripps Institution it seems possible that similar spatial changes, in the plant-phosphate picture in particular, occur outwards from an upwelling or "dome" region in the tropical Pacific.

Thus the commoner methods of statistical analysis, although they are useful in indicating, initially, factors which may be affecting production, are not so useful in more detailed work. This is because in, say, a multiple correlation, the variables representing the different ecological factors must be capable of transformation into *linear* (or additive) relations. But the various mathematical forms for the causal relations, although they are rather dubious, have one common property—the relations are always *nonlinear* owing to the complexity of the interactions in the biological systems. It is this essential nonlinearity which makes it necessary to set up a theoretical picture before the data can be analyzed quantitatively, and which limits the value of data collected rather at random, for example, during the grid type of survey when changes in the population are occurring.

Because of these difficulties with time changes, the so-called steady state conditions are often considered theoretically, and looked for in natural events when the populations might be expected to be stationary or to change only slowly with time. Yet situations where this could be thought to hold are often masked by the great variability found in the plankton samples in an area which hydrographically appears homogeneous.

Since this variability is a major difficulty, I shall try to show some of the problems of sampling and of interpretation which it raises. By thinking of phytoplankton in terms of its carbon content, we imply that it is essentially passive and uniformly composed, and so the question arises as to whether its variability can be explained by the variations in its environment. These can be studied by starting from the hypothetical steady state conditions of the deterministic model and producing simplified forms of stochastic processes by introducing natural or random fluctuations. Thus one of the main controlling factors is the variation in daily radiation. I shall assume that the mean photosynthesis per unit of population in the euphotic zone is proportional to the total radiation. This is rather extreme since there will be damping effects due to near-surface inhibition by strong light and to changes in the depth of the euphotic zone due to the size of the population. However, it is a first approximation, and Fig. 3 shows the effects using light data from Aberdeen in May and June, 1957, expressed here as deviations from the average over the period considered. It can be seen that quite large day-to-day fluctuations during the first half do not produce very large changes from the mean in the plant population. It is only in the second half, when there are periods of consistently high and then low intensities, that the population changes significantly. Thus a week with good sunshine increases the population by a factor of three.

This also shows the complex relations between light and pro-

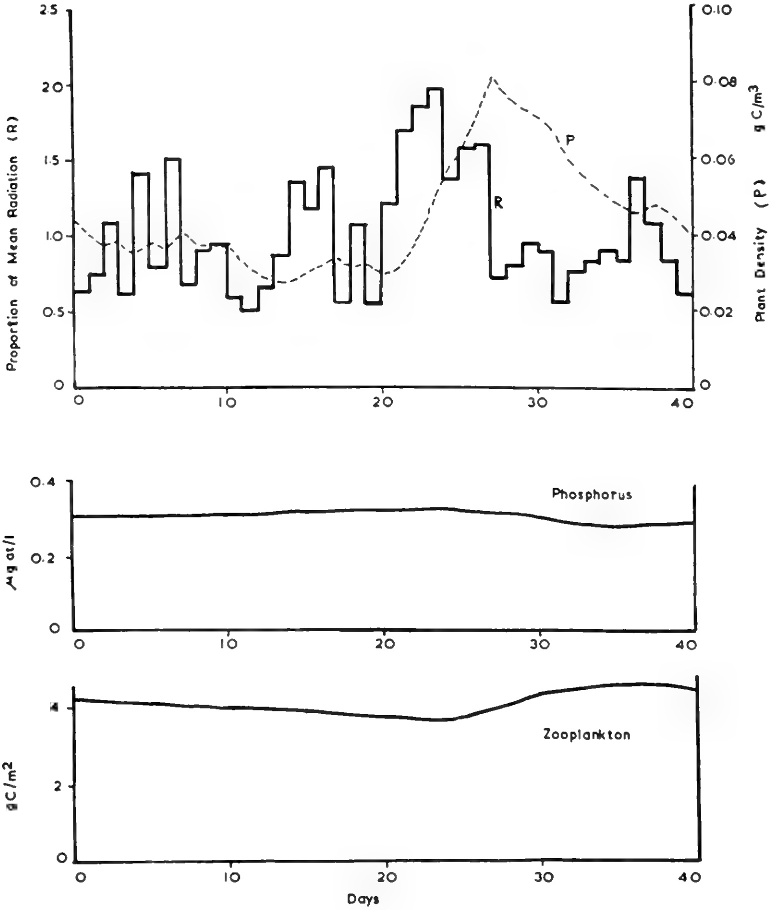


Fig. 3. The effects of natural light data introduced into the theoretical model.

duction, for although the production per unit of population on any day depends mainly on the light during that day, the total population itself depends on the light during, say, the previous week. Thus a C^{14} *in situ* measurement is a complicated function of light over a fairly long period of time. Again the probability of the population varying with light depends on the nonrandomness of runs of bright or dark days. Even with British weather such runs of five or more days do occur quite frequently. This in turn tends to upset the use of average values such as Kimball's tables. Figure

3 also gives the corresponding changes predicted by the model for zooplankton and phosphate. This shows how the variability of the light which is partly smoothed in the plant distribution is even further smoothed out in the nutrients and animals so that changes in light contribute very little to their variability.

From this point of view, zooplankton variability which is such a marked feature, must be thought of as being imposed by the behavior of the animals themselves. It has been shown by Winsor and Clarke (1940) and Barnes (1952) that in temperate waters, the variable distribution of plankton in net hauls tends to be normalized by a logarithmic transformation. Thus, by using their estimate of the variance, it is possible to imitate the patchiness of the herbivores by transformation from a table of random normal deviates, if it is assumed that on each day the value is taken as a random deviation from the value on the previous day. This produces clumped distributions as shown in the two sequences or runs in Fig. 4. Both of these show how the patchiness produces significant depletion of the plant population if the patches remain in contact with the same plant population for about a week. The phosphate curves in Fig. 4 show again that these changes have little effect on the nutrient concentration, so that the chemical sampling would give an impression of uniformity. These plankton changes could be considered as typical of changes occurring at the same time over an area of sea and, as in the earlier example, pairs of values could correspond to pairs of samples collected over this area. Figure 5 gives the plots of these values and demonstrates again that, with conventional sampling, apparent randomness can result from quite well-defined processes.

These two factors, light and zooplankton patchiness, tend to produce variability in plant distributions. There is a third factor, the lateral mixing of the water, which tends to decrease this variation. To estimate this effect I have used an expression for lateral eddy diffusion from a center derived by Joseph and Sendner (1958). By assuming that grazing is zero at the center and increases with distance from it, it can be shown that for a given production rate per unit of plant population there is a gradient in plant concentration for which the net growth of the population

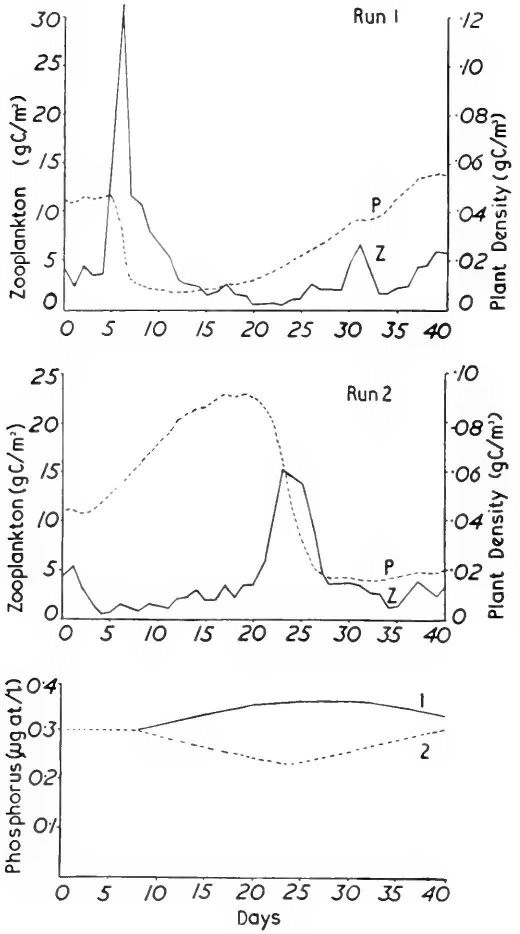


Fig. 4. The effects of random zooplankton variations (Z) on the plants (P), and on phosphate-phosphorus, as derived from the theoretical model.

balances the effects of diffusion. Thus, on this basis, for a growing patch, the gradients must be less steep than this limiting value. The gradients are expressed in exponential form so that the plant concentrations increase by a multiplicative factor over equal distances. For a factor of three, which is often used in drawing contours, the limiting relation is that the distance in kilometers between such contours equals 2.2 divided by the production rate

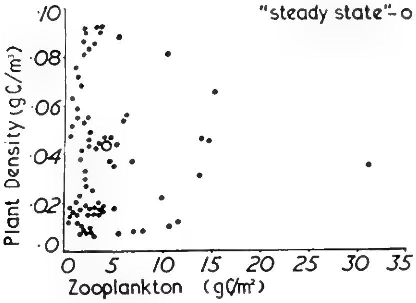
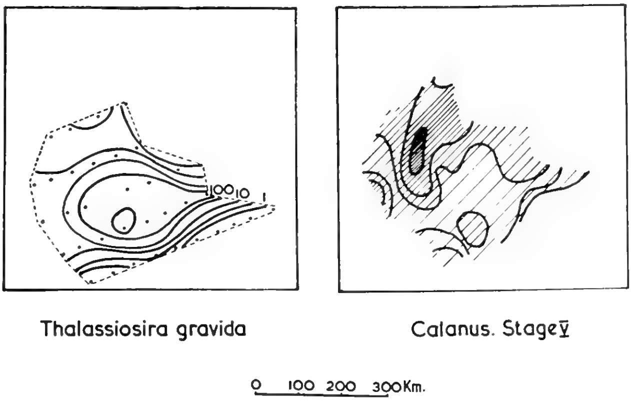


Fig. 5. The relations between the daily values of plants and zooplankton taken from the two runs in Fig. 4.

per unit of population. Thus for a growth rate of 50% the distance between contours is 4.4 km whereas for 5% it is 44 km. As an example of such distributions I reproduce in Fig. 6 two charts from Cushing's (1955) study of production in the southern North Sea. The dominant diatom *Thalassiosira gravida* and the main grazing component, *Calanus*, are shown contoured by factors of about three. The division rate of the diatom is given as 40%, which would mean a minimum distance between contours of 5.5 km. Along the southern edge of the patch where the zooplankton are scarce, the distance is about 8 to 10 km. The zooplankton patch, although it does not have such steep gradients, has about



Thalassiosira gravida

Calanus. Stage V

Fig. 6. Examples of plankton patchiness (Cushing, 1955).

the same dimension. For the very simple calculations made here, this is close enough and on the right side of the minimum, and suggests that an approach of this type gives an indication of the expected dimensions of patches.

It implies that in inshore areas, where the production rate is often high, the marked degree of patchiness may be due partly to the above reasons as well as to the "patchiness" of the hydrographic features. To be even more hypothetical, it may also be that zooplankton patchiness of such organisms as *Calanus* can provide a means for grazing on higher than average plant concentrations and thus permitting rather lower numbers of animals to have a higher feeding rate than they could have if grazing were evenly distributed. The importance of this, through the dependence of egg laying on food supply, has been shown by Marshall and Orr (1955). On the other hand, for areas with low productive rates, the patches could have only very small gradients and so be situated at large distances apart. As these dimensions increased, it is possible that the advantages of patchiness in animals would decrease on account of the large horizontal distances involved so that in very poor waters patchiness would disappear altogether, as seems to be the case in unproductive tropical areas.

In this way, I have tried to show roughly how the time and length dimensions of plankton changes may depend on production rate per unit of populations. For temperate waters in particular it suggests that the grids of stations often used, and repeated at monthly or even weekly intervals, can be expected to show considerable apparently random features. On this basis, samples on successive days, or at distances of 10 km, may be required to show up the detailed patterns.

A consequence of this description of patchiness is its relation to pelagic fish, such as herring, which feed on the zooplankton. Since the small-scale relations between fish and zooplankton may be similar to those between the animals and the plants [with the same processes of aggregation, grazing, and disengagement as Cushing (1955) and Manteufel (1941) have shown for herring], conventional sampling again can be expected to produce the same apparent lack of any real relation. It seems likely that the time and length dimensions of herring concentrations and movements will be of the same order as the plankton ones, and this statistical distribution is all that one may be able to predict about their detailed behavior.

In studies of this kind, some of the variability can be removed by going to the opposite extreme from a homogeneous hydrographic situation and choosing an area where there are very large hydrographic changes in short distances. This is found at the edge of the Baltic outflow up the Norwegian side of the North Sea, where a layer of cold fresher water overlies the typically warmer and more saline North Sea water. In early spring this layer is very productive when the rest of the North Sea is not due to the latter's vertical homogeneity. The resulting distributions for a small part of this edge are shown in Fig. 7 where the stations are 10 miles apart. In the temperature chart the position of the edge was found with a surface thermograph. The phosphate and chlorophyll data show how marked the production changes are at this edge. On the fourth chart the edge has been drawn in and shows that the her-

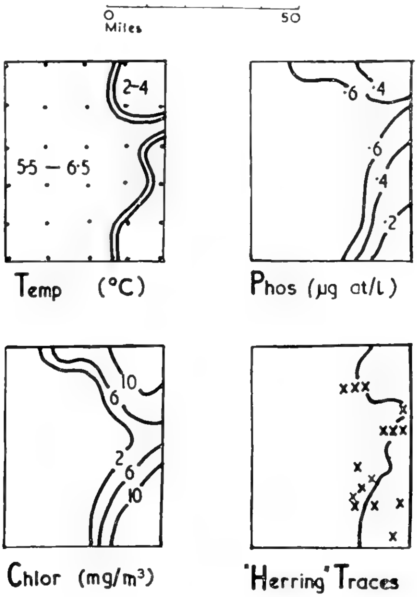


Fig. 7. Distributions at a sharp hydrographic "edge."

ring distributions lie close to or just under the cold edge. The explanation of these concentrations is probably in terms of a balance between the tendency of the fish to enter the cold water for food and an opposing reaction against the low temperatures, corresponding to the experimental result that herring tend to stop feeding below 4° C. This type of extreme situation shows how one dimension of randomness is removed since, although the fish are probably "patchy" along the edge, they are nonrandom across it, making it easier to study some of the relations between productivity and herring distributions.

As a final example, there is the problem of the adequacy of chlorophyll data in studying detailed vertical distributions of the plants. Saijo and Ichimura (1959) and also Menzel and Ryther (1959) describe chlorophyll maxima at the foot of the euphotic zone and attribute this to the effects of sinking. Steele and Yentsch (1960) have shown that the sinking rate would have to decrease in the region of these maxima, and we have found some experimental evidence for this in terms of a decreasing sinking rate when nitrogen-starved cultures are enriched. This would correspond to the higher nutrient concentrations found at the foot of the euphotic zone. In the sea, however, there will generally be vertical variations in species composition. The dominance of different species at increasing depths may be due to the effects of sinking on a succession of species growing near the surface, but it may be the result of differential adaptation for growth at different depths. Thus as Menzel and Ryther point out, an understanding of these changes is necessary before an explanation in terms of sinking can finally be accepted. Some of the complexities of the vertical distributions of individual species or groups is to be found in the work of Bernard (1956, 1959).

In these various examples I have tried to show the kind of difficulties which arise in interpreting ecological data relating to primary production. The theoretical pictures which are sometimes dignified by the title "mathematical models" are very idealized descriptions of what may happen. They have to use such simplifications as the concept of a two-layered sea or of equal grazing at all depths by the zooplankton. Yet, because of the complex relations between the different factors involved, they are a necessary link between the data and that other set of idealized pictures, laboratory experiments. The two are complementary and together can allow some insight into the causal relations operating in the sea.

However, if there is to be any hope of showing whether the hypothetical relations are actually occurring in the sea, one must make a very careful choice of areas to work in. It is no longer true that any part of the sea can be made to yield information that is useful from this point of view. For a randomly chosen area, the hydrographic structure during any period of time is likely to be very complicated and difficult to understand. As a consequence the biological cycles at different times or places will not be sufficiently similar to be considered together nor sufficiently different to be easily separable.

Thus the amount of information that can be acquired about the production cycle will depend on the hydrographic information available and on the way in which this information can be expressed as a fairly simple picture. We need to use areas that approximate to two-layered seas: regions that are laterally homogeneous and without the troublesome occasional incursions of different water masses; sharp hydrographic edges; or such special cases as the "dome" regions studied by Holmes which may correspond to diffusion of nutrients from a centre.

Yet, although the choice of areas is based in hydrographic considerations, the distribution of sampling is not. The classical concept of lines or grids of stations at widely spaced intervals of time and distance, which has been the main method of revealing hydrographic patterns, is not necessarily suited to plankton problems. In the extreme case of patchiness in temperate waters, very detailed sampling in a very homogeneous hydrographic area may be needed to show up the biological patterns in this process.

Similarly, the usefulness of data on primary production for fishery problems is still limited. One is likely to get the sort of randomness already described, if the problems are chosen on the basis of the economic importance of the fisheries rather than on the probable simplicity of the main features of the environment. In this way small or isolated fisheries may be the best testing places for hypotheses about the relations between the fish and the basis of their food supply.

I realize that in this paper I have concentrated more on the problems than on the achievements in this field and have said too little about our general understanding of production in different seas. This is the necessary background for our present concern with detail and with particular anomalies in methods which have been generally successful. Also, in the problems I have mentioned, I have unduly stressed those involving the quantitative analysis of data at the expense of more biological questions. Particularly, I have neglected the difficulties of studying the plants in terms of the individual species that make up the populations we think of as chlorophyll or carbon. I do not think this is entirely a personal bias and I feel that the recombination of these two aspects will be a necessary and most difficult future problem.

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The Balance between Living and Dead Matter in the Oceans

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IN discussing the balance between the living and dead matter in the ocean, the problem should be reduced to one of interrelationships or, better still, to a web of interrelationships. These ultimately result in a quasi-constant standing crop of plankton organisms. Recently Cushing (1959a, b) and Steele (1959) proposed some reference lines for such a system. In their papers, there is frequent mention of the large gaps in our knowledge of the life processes in the sea and even of the metabolism within the organisms themselves. Hence, it may seem premature to speak about the balance of matter in the sea. Despite this, I am going to do so in order to stimulate thinking about such matters.

First, the different actors in the system must be presented. There are at least five of them: phytoplankton, zooplankton, limiting nutrients, light, and the turbulence of the water. A sixth one, "tripton," that is, detritus plus inorganic particulate matter has hitherto been known only by name.

Phytoplankton

The taxonomy of the phytoplankton, as well as some of its biological, ecological, and physiological factors, is well known. For example, the work of Braarud *et al.* (1953) in 1948 gives an excellent picture of the population over the entire North Sea. Only one other survey is comparable, but it is for a much larger area, the South Atlantic (Hentschel, 1936). Both these investigations of necessity lack one most important component, time.

Obviously, much good work on the phytoplankton cycle has been carried out at coastal stations throughout the entire year. Lohmann (1908) was perhaps the first, who made not only a quantitative census of the phytoplankton species but also calculated the total biomass, expressed as cubic millimeters per 100 liters. He likewise compared the food requirements of the standing zooplankton crop with the available abundance of the phytoplankton and recognized that during the winter the zooplankton must feed on detritus to a very large extent.

Despite this early work, many problems centering on the phytoplankton population in the oceans are still unsolved. Our attention must first turn then to the activities of phytoplankton, the first component in the system considered here. The dark-light bottle method for oxygen production and that of C^{14} fixation were milestones in the development of our understanding of its role. Yet there is much more to be done. Productivity, for example, must be correlated with the standing crop. In short, we must know the rate of assimilation more exactly. This varies between three and thirty in relation to the life histories of individual phytoplankton species. It may be possible to correlate productivity not only with chlorophyll concentration but also with the truly active substance within the cells, the proteins.

In general, phytoplankton assimilates material until no more nutrients are present in the surrounding water provided that there is sufficient light available and that there are no inhibiting substances present to prevent this activity (Steemann Nielsen, 1955; Jørgensen, 1956). This activity of the phytoplankton may utilize all the specific nutrients which then become limiting factors within a few days or perhaps a few weeks. In the sea, this process is much more rapid than on land. Unfortunately, our knowledge of the assimilation potential and more especially of the reverse, the decomposition under natural conditions, is relatively limited. This has been discussed during the Congress by Steemann Nielsen (1959). We must try to relate these two processes with the truly active substance in the phytoplankton, the proteins. Special attention should also be given to the respiration of the phytoplankton when there is insufficient light.

Zooplankton

The second actor, the zooplankton, has held the attention of so many zoologists and zoological specialists engaged in general marine research that the systematics seem fairly well known. In addition, we are somewhat familiar with its distribution in space and time and with its physiology. Between the pioneer work of Lohman (1908), who determined the annual cycle of individual species and the zooplankton volumes, and the excellent work of Vinogradov and Bogorov, who investigated the quantitative distribution of the zooplankton biomass, the methods have markedly improved, and valuable results have now been obtained at many localities in the deep sea. We may cite Bogorov's (1957) figures for the biomass of living zooplankton, namely an average at the surface (0–50 m) of almost 50 mg/m^3 and between 6000 m and 8500 m of only 1.7 mg/m^3. Very little is known, on the other hand, about the physiological responses of the zooplankton, and not enough about its metabolism and its nutrient requirements. Therefore the work of Conover (1959) on the respiration rate of copepods is of greatest importance.

In connection with these unanswered questions, I draw your attention to an important problem, the base of reference to be used in all metabolic measurements. We cannot refer to the length of the body or the wet weight of an organism because these units contain many inert materials, such as the skeleton, reserve material, and differences in water content. In this connection, we may cite MacFadyan's (1957) *Animal Ecology*, which has an excellent discussion based on terrestrial organisms. C. Barker Jørgensen (1955) has added to this by summarizing what is known of the food intake of marine filter-feeding animals and based some of his computations on nitrogen. With modern methods, we can make basic analysis for proteins and thus improve our knowledge in this area.

Limiting Nutrients

The quantity of limiting nutrients in ionic solution is the third actor. Everybody engaged in marine research knows the role of nitrogen and phosphorus and other elements important in biology, such as copper, manganese, cobalt, and iron, as has been so ably summarized by Harvey (1955). The quantitative distribution of the major constituents is best known by the inorganic compounds of the total phosphorus. As an example, I draw your attention to the lengthy description of the PO_4^{3-} - P concentrations in the South Atlantic (Wattenberg, 1957).

The respiration processes of zooplankton and bacteria and the processes which bring nutrient-rich water to the surface are of particular interest. Everybody knows the areas of upwelling in the ocean. The activity of the large currents should also receive special attention, e.g., because on their left-hand boundary in the northern hemisphere, deep water is brought to the surface layers. Thus, there is a eutrophic zone closely connected with mixing caused by these currents. We might add that the role of heavy storms of long duration in the ocean should not be underestimated in the part they play in maintaining the supply of nutrients. In addition, we urgently need better methods of analysis for the different components of total phosphorus and for total nitrogen in ionic solution. These new techniques are essential if we are to make analyses on shipboard in sufficient numbers.

One question mentioned by Lucas (p. 499) is of the greatest importance, namely the role of organic substances in solution. Their activity takes place in two different ways. They may contribute to the nutrition of filter-feeding animals only when adsorbed on suspended particles. They become concentrated there and then may serve as the foci for the development of a population of bacteria. Secondly, organic substances may act as inhibiting factors as shown by Steemann Nielsen (1955) and by E. G. Jørgensen (1956).

Light

We know the role of light, the fourth component, as the source of energy for the production of organic matter and for the phototropic orientation of animals and plants in an aquatic environment. Jerlov (1951) has done much good work in this field. We would, however, be very happy from the viewpoint of basic productivity in the oceans were we to know more about the annual cycle of light in different areas of the oceans and at various depths. These observations could well be carried out aboard weather ships together with measurements on the depth of the thermocline. In this connection, too, I may point out that marine biologists should pay much more attention to the dynamics of the water masses in the oceans, especially to their vertical movements and to their heterogeneous physical and chemical characteristics, as well as to their past "history."

Interrelationships

We must next consider other interrelationships. First, let us examine the activity within the phytoplankton cells themselves. When sufficient light is available, they will grow rapidly until the major nutrient constituents in the surrounding water fall below the minimum concentration required for their physiological processes. In any given body of water, the amount of living matter increases while that of phosphorus compounds continuously decreases. Under no conditions does a steady balance obtain, except in its end state, when no more phosphorus is available. Here, then, we do not have a static balance but a dynamic one. But even in this end state, when all the nutrients in the water have been depleted and also those adsorbed as an "internal reserve," one cannot speak of a stable state or an exact balance. The phytoplankton cell itself continues to metabolize, the phosphorus released is a measure of the decomposition of the living matter when there is insufficient light. During the day, organic substances are rebuilt with the phosphorus lost during the night. Thus, the balance is not static, even when the total number of cells remains constant. Hence, one can speak of an "oscillating balance." The period and the amplitude for this system depends on the length and intensity of the light exposure as well as on individual factors "of activity."

If we now turn from a single cell to a pure culture, we may perhaps expect that these oscillations are somewhat stabilized by the different sizes and ages of the cells. This supposition may be carried farther when we have a standing stock of different species and even classes of phytoplankton organisms. Here we urgently need an exact analysis of the biochemical and physiological processes which are taking place. It would be interesting to learn whether the total quantity of organic matter, especially of proteins, oscillates even when the total number of cells remains constant.

Dotterweich (1940) concluded that even an individual organism cannot attain a balance that is really stable because of the different processes of metabolism. In a biocoenosis, each individual is only one component, but the total stock may become more stable with an increase in the number of different components. According to Friederichs (1930), a balanced biocoenosis is merely theoretical. The more one tries to balance it, the more the equilibrium is disturbed. It should also be pointed out that every balance must be exactly defined. In our case, this means that the total quantity of living matter must be constant when environmental factors remain unchanged.

Let us continue with the discussion of the model. Normally, a population of phytoplankton is dependent on the dynamic water movements in the oceans, especially in the surface layers. Owing to turbulence the phytoplankton is transported into various layers with different light intensities for varying periods of time. Thus, the oscillating balance of a single cell may be disturbed and depressed when the cells are carried away from the zone of optimum assimilation. Then decomposition, which forms a part of the total respiration, becomes larger and more phosphorus becomes available. Because of very different activities, the oscillations increase in period. Steele (1959) has demonstrated four different stages in the interaction between the standing stock of phytoplankton and the upper turbulent layer. The extent of this layer becomes critical when the uptake of physiological energy does counterbalance the cell requirements. Then light becomes the limiting factor, because the ordinary nutrient constituents which may at times be limiting are available in sufficient quantity. The oscillating balance is actually an open unbalanced system. Here it may be said that a relationship exists between two entirely different forms of energy.

In this connection the upper limit of total phytoplankton abundance under one square meter may be of interest. In Burlew's tank experiments, the maximal concentration may reach 3000 mg of chlorophyll under a square meter, if we may assume chlorophyll as representative of the total phytoplankton biomass. In a lake, Gessner (1949) found a maximum of 2000 mg chlorophyll per square meter. In a fjord in Kiel Bay, there was 280 mg/m^2 calculated only for the trophogenic layer. The latter yielded 62.5 g of dry organic matter in a layer only 2.5 m thick. The development of phytoplankton is actually a self-limiting process. Extreme concentrations only appear to be in a stable balance with their environment. We must consider the oscillations and also the possibility of rapid decomposition when zooplankton preys upon it or when any other environmental factor stimulates the further growth of the standing stock.

The zooplankton has a relatively simple relationship to our problem of balance, because the reaction is one-sided. As long as particulate nutrients are available, the zooplankton will feed on it and grow as quickly as biological conditions allow. Here only one example will be considered, under conditions in which inert material plays a role, namely, when the zooplankton feeds on detritus. Detritus, also called "tripton," serves as an adsorbent for organic matter in solution, but there are unfortunately no investigations on its role in the cycle of organic substances in the sea. From investigations, such as those of Marshall and Orr (1955), we may estimate its value. Jannasch (1954) has photographed the bacterial population on the surface of detritus, thus suggesting its nutritive value.

Detritus is the only source of food for all filter-feeding animals in the deep sea, including the sediment feeders. Over sufficiently large areas and periods of times, we might expect a dynamic equilibrium between the detritus and filter feeders in the deep sea. This differs principally from that mentioned above between the phytoplankton and its nutrients because in the former no cycle exists.

In the relationship between living and dead matter, respiration in the zooplankton is much more intense than in the phytoplankton. It should be mentioned that Cushing (1959) pointed out the role of the zooplankton in the "scattering layer" and compared it with the bottom living animals in the shallow sea.

Because of its relatively high metabolic rate, the zooplankton greatly affects the oscillations of the dynamic balance between living and dead material. When a large swarm of copepods grazes on phytoplankton, only 10 to 20% of this food is actually transformed into zooplankton biomass. The remaining 80% is utilized during metabolism or becomes detritus. In either case, decomposition is relatively rapid. Because of the marked vertical movements of the zooplankton, one water layer may become enriched with the products of decomposition just mentioned. It is thus removed from the layer where it originated. We know that such accumulations actually exist at depths of, for example, 200 to 400 m. In this way, the oscillating balance is transferred downward. Here, then, the dynamics of the water may serve to distribute materials evenly throughout the mass.

We should next consider how a population reacts in a balanced system. Even should the individuals within it remain stable, it is possible that a population, composed in certain proportions may almost reach an equilibrium. In a limited body of water the decomposition of the organic substance may equal its assimilation. This process may best be followed by the energy involved. I believe, however, that the oscillating balance of the phytoplankton, which is transferred deeper through grazing by the zooplankton, is always disturbed especially by the difference which is needed to decompose compounds in solution. In order to get a quasi-stable state, we must choose an area and a period of time sufficiently large such as the Atlantic Ocean. Then allochthonous substances will not be important. The general bare line of the population density would be relatively constant there. Unfortunately, there are insufficient analyses of the total biomass to prove this point with actual data.

Even if we cannot strictly observe a stable balance between living and dead matter in the ocean, we can determine certain irregularities in the population as a result of the action of the many different processes. In a wide sense we may take this web of relationships as a "parabalance" indicating by this term that a stable balance does not exist but that the regularities mentioned above suggest a relatively constant population as a result of the environmental conditions. It will be a long time before we can draw charts of the total biomass in any one ocean for each month of the year. Indeed, even when we do this, we must always remember the heterogeneous conditions and their dynamics.

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The Physical Chemistry of Sea Water

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IN discussing the physical chemistry of sea water, I shall consider especially the equilibria in the ocean, and the form in which the various elements are present in sea water.

Average Composition and Volume

In discussing chemical equilibria in a solution, it is convenient to express all concentrations in the same unit *M*, mole/liter, as is used in the equilibrium constants. Table I gives the average concentrations of the major constituents in sea water (Sverdrup *et al.*, 1942, p. 173). Evaporation or fresh water may vary these concentrations somewhat, whereas their ratios are as a rule maintained practically constant.

TABLE I. Major Constituents of Sea Water

	c, mole/liter	log *c*		*c*, mole/liter	log *c*
H_2O	54.90	1.74			
Na^+	0.47015	−0.33	Cl^-	0.54830	−0.26
Mg^{++}	0.05357	−1.27	SO_4^{--}	0.02824	−1.55
Ca^{++}	0.01024	−1.99	HCO_3^-	0.00234	−2.63
K^+	0.00996	−2.00	Br^-	0.00083	−3.08
Sr^{++}	0.00015	−3.82	F^-	0.00007	−4.15
			(H_3BO_3)	0.00043	−3.37

For the acid-base and redox equilibria we shall use the average values (Harvey, 1957, p. 155; Sverdrup *et al.*, 1942, p. 210):

$$\mathrm{pH} = 8.1 \pm 0.2 = -\log \{H^+\}$$

$$\mathrm{pE} = 12.5 \pm 0.2 = -\log \{e^-\}$$

These are average values for the bulk of the ocean; in isolated pockets of the ocean, or in places with strong biological activity, larger deviations may occur. The average temperature seems to be about 5°C, the density is taken as 1.024 g ml^{-1}, and the average depth as 3,800 m, which gives an average pressure of nearly 200 atm.

The total volume of the ocean has been estimated as 1.37×10^9 $km^3 = 1.37 \times 10^{21}$ liters. The volume of this solution and of the gas phase and solids with which it may react seems somewhat unwieldy to an ordinary chemist. With your permission, in the following I shall divide all these amounts by 1.37×10^{21}, and thus consider 1 liter of average ocean water and its share of the atmosphere and the sediments.

Atmosphere

The total mass of the atmosphere has been estimated as 5.13×10^{21} g. With an average molecular weight of 28.97 and with the partial pressures 0.7809 atm for N_2, 0.2095 atm for O_2, 0.0093 atm for Ar, and 0.00030 atm for CO_2, we find that the share of 1 liter of sea water will be 0.1293 mole dry air (3.16 liters at 25°C, 1 atm or 2.90 liters at 0°C, 1 atm), containing 0.1010 mole N_2, 0.0271 mole O_2, 0.0012 mole Ar, and 0.000039 mole CO_2.

What Determines the pH?

One of the first questions that an equilibrium chemist will ask is this: What makes the pH equal 8.2? A common answer is that pH is determined by the buffering of the H_2CO_3–HCO_3^-–CO_3^{--}, and to some extent also by the $B(OH)_3$–$B(OH)_4^-$ system. This answer is correct in one respect. If one removes 1 liter of sea water from its surroundings and adds strong acid, almost 3 mM H^+ will be used up in transforming HCO_3^- to H_2CO_3, and in the meantime the pH remains about 8 to 6; only after that, the H^+ added will remain as such in the solution, and pH will drop to 3 or 2. Similarly, if strong alkali is added, almost 3 mM OH^- is needed to transform $B(OH)_3$ to $B(OH)_4^-$, and HCO_3^- to CO_3^{--}, which, incidentally, precipitates as $CaCO_3$.* Now, a buffer concentration

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* If more OH^- is added, $Mg(OH)_2$ precipitates. I have been told, however, that the ocean never seems to have been at equilibrium with solid $Mg(OH)_2$.

of less than 3 mM is not too impressive compared with the total concentration of ions in the solution, which is more than 200 times greater.

If we consider the origin of the ocean, we might say that the ocean is the result of a gigantic acid-base titration: acids that have leaked out from the interior of the earth, HCl, H_2SO_4, CO_2, are titrated with bases that have been set free by the weathering of primary rock. In this acid-base titration, volcanoes against weathering, it would seem that we are about 0.5 per cent from the equivalence point. This, by the way, is better than most students of chemistry do in their first titrations.

It seems that either the pH of the ocean is somewhat precarious, or there must be some other factor that determines the pH by buffering. In the following, one possible factor will be pointed out.

Mixing a Model Ocean

It may be well to try to consider all the various substances that have been of importance in the formation of sea water.

Goldschmidt (1933, 1937a) started from estimates of the average composition of igneous rocks, of sediments, and of sea water, and from estimates of the quantities of sediments and sea water. He came to the conclusion that for each kilogram of ocean water, some 600 g of primary igneous rock must have been decomposed.

Table II is based on Goldschmidt's estimates for the major constituents, recalculated to the unit we are using, mole per liter of ocean water, and rounded off to 0.01 mole. For each element amounts derived from primary rock and present in sediments and sea water are given. Some volatile elements, especially H, C, Cl, and S, are found in greater quantities in sea water than would correspond to their concentration in igneous rock. Hence, they must have come chiefly from the interior of the earth and concentrated at the surface by distillation, for instance through volcanic activity, which may set free H_2O, HCl, HBr, HF, CO_2, SO_2, and $B(OH)_3$.

In the following we will use Goldschmidt's figures; other estimates give somewhat different numbers but do not seem to change the main features of the picture.

TABLE II. Number of Moles of Major Components Corresponding to 1 Liter of Sea Water (Calculated from V. M. Goldschmidt's estimates)

	From Rock	Volatile	In Ocean (*c*)	In Sediments (*n*)[a]
H_2O	—	54.90	54.90	—
Si	6.06	—	—	6.06
Al	1.85	—	—	1.85
Cl	0.01	0.54	0.55	—
Na	0.76	—	0.47	0.29
Ca	0.56	—	0.01	0.55
Mg	0.53	—	0.05	0.48
K	0.41	—	0.01	0.40
C[b]	0.02	0.53	—	0.55
O_2	—	0.03	(0.03, g)	—
Fe	0.55	—	—	0.55
Ti	0.06	—	—	0.06
S	0.01	0.06	0.03	0.04
F	0.03	?	—	0.03+?
P	0.02	—	—	0.02
Mn	0.01	—	—	0.01
N_2	—	0.10	(0.10, g)	—

[a] The sediments are estimated to contain 0.46 mole $CaCO_3$ and 0.09 mole $MgCO_3$ (Goldschmidt, 1933).

[b] Only the carbonate C has been considered, not coal or bitumen.

In an attempt to understand the reactions that may determine the composition of "model" sea water, we may imagine a process in which 1 liter of sea water, with the corresponding amounts of solids and gas phase, is prepared by mixing the constituents, starting with the more abundant ones. We shall try to imagine what the result would be if real equilibrium were obtained after each addition; we may then compare this with what is known about the composition of the "real" average sea water, sediments, and air (Fig. 1).

Please note that I did not state that there is a true equilibrium in the real system. It would be identical with the model. I only suggested that it may be worth while to try to find out what the true equilibrium would be like, and that one might learn something from a comparison with the real system. We shall often find that sufficient data are lacking to make the discussion very precise.

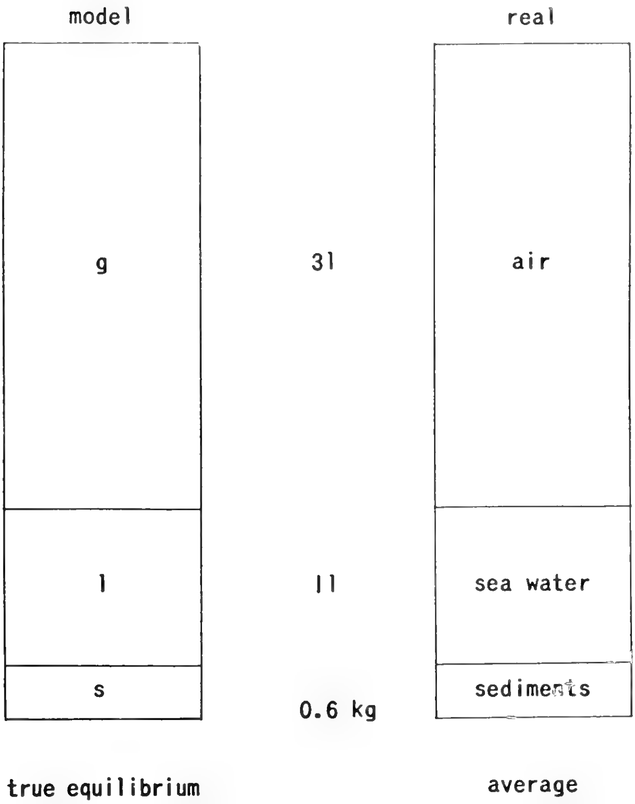

Fig. 1. Right, real system: 1 liter of sea water and the corresponding amounts of sediments (0.6 kg) and air (3 liters). Left, model under discussion: the same amounts of the various elements brought to true equilibrium (excepting N_2).

Neither the laboratory data on chemical equilibria (needed for the model), nor the geochemical data (for the real system) are always as accurate as one might wish. Still, it may be worth while to try this approach.

Objections to Equilibrium Model

Perhaps some comments should be made on the approach of the real system to equilibrium. One might object that stirring is not so good as in most laboratory work. However, admitting a rotation period of 1000 years for the ocean, 500 million years give half a million rotations, which would correspond to a rather thorough mixing of the liquid phase.

Of course, only the uppermost layer of sediment is in good contact with the liquid; the lower layers of sediment are practically cut off from contact with the sea water. On the other hand, each particle of a marine sediment has once been in the upper layer, and has even been suspended in sea water, and has thus had some chance to approach equilibrium with it.* Moreover, it seems that a considerable part of the present sediments have been repeatedly in contact with sea water. Excepting a few areas with primary rocks, it seems that most present-day weathering and erosion works on old sediments which will thus eventually be re-equilibrated with the ocean.

Another objection is that the *temperature* is remarkably uneven in the ocean, in comparison with laboratory experiments: it varies from around +30°C close to the surface in tropical waters to less than 0°C in other parts. This is especially important for equilibria with solid phases; equilibria between species in solution usually adjust themselves more easily.

In a first approximation one might perhaps use some "efficient solubility product," valid for the temperature where a deposit is formed, usually perhaps somewhere close to 0–5°C. We may remember the "law of the cold wall": if a condensable vapor is brought into an empty container with uneven temperature distribution, it will condense on the coolest wall, and the partial pressure in the whole vessel will correspond to saturation at the temperature of the coldest wall.

The equilibria are also influenced by the *pressure*, which varies from 1 to 1100 atm in the ocean, the average being perhaps 200 atm. In general, the solubility product of a salt will increase with pressure because the molar volume is less in solution than in the solid (see next section). At first glance, one might then perhaps believe that, in a steady column of sea water of uniform temperature, a solid like $CaCO_3$ would dissolve at the lower end and precipitate at the higher end. This, however, would have been a

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* Dr. Shishkina (1959) reported that the interstitial water in some deep-sea sediments does not change its composition over periods of 100,000 years, which may indicate that the precipitate is practically at equilibrium.

good basis for a machine of perpetual motion. In reality, the lower solubility at low pressures would be more than counterbalanced by a concentration gradient which would make the concentration lower at the upper end. The tendency would be for the solid to dissolve at the upper end and precipitate at the lower: the equilibrium position of a heavy solid is, after all, at the bottom of the column. Currents in the ocean will, however, prevent this diffusion equilibrium from being achieved, and so one may imagine that water from the depth, saturated with a certain solid, is lifted to layers with lower pressure where the solid will precipitate.

In our imaginary model, we must treat the differences in pressure like those in temperature and work with some average or effective equilibrium constant.

Finally, it may be said that the *life* processes will take the sea water far from the equilibrium composition. This is true especially in the surface layer, containing perhaps 5% of the bulk of the ocean, where the concentrations of C, P, Si, and some other elements may be considerably changed. In the remainder of the ocean, however, it seems that the processes working toward equilibrium will predominate.

There are also pockets in the ocean, like the depths of the Black Sea, with stagnant water, oxygen deficit, and low pH: these exist, however, only because they have so little contact with the remainder of the ocean. We shall neglect these in the following discussion, which may, perhaps, give a useful first approximation.

Data Used; Correction Terms

The concentrations of various substances in sea water have been taken from Sverdrup *et al.* (1942, pp. 173, 176), Harvey (1957, pp. 140, 224), and Richards (1957). Goldschmidt's estimates on the amounts of various substances in primary rock and sediments have been taken from the original papers (1933, 1937a,b) or as recalculated and completed by Rankama and Sahama (1950, pp. 39, 295). In addition, some information on the composition of pelagic sediments has been taken from a paper by Goldberg and Arrhenius (1958).

The equilibrium constants for solubility, complex formation, or acid-base equilibria have mainly been taken from the compilation of Bjerrum *et al.* (1958) and from supplementary tables which are being kept up to date in Stockholm. The equilibrium constants for redox reactions are taken from a compilation which is being prepared in Stockholm and which will eventually be published. In these tables, full references are made to the original literature; in this paper, this is done only occasionally.

The original equilibrium constants are very often those calculated from "zero activities" (based on an infinite dilution as the standard state) in the law of mass action. In general, measured values of pH and pE can be assumed to correspond to zero activities of H^+ and e^-. For other species, the zero activity constant should be corrected with activity coefficients for the medium of ocean water. We shall use, as a very rough estimate, $\log f_1 = -0.2$ for univalent ions, and $\log f_2 = -0.8$ for bivalent ions.

Some equilibrium constants given in the literature refer to an ionic medium, such as $0.5M$ NaCl; or 0.5, 1, or $3M$ $NaClO_4$. The corrections from these media to sea water should be considerably smaller, and have been neglected here in comparison with the variation with temperature and pressure.

All equilibria are more or less dependent on *temperature.* The equilibrium constants are often determined only for 25°C, whereas 5°C is closer to the real average temperature. As seen from some examples in the text, where $\log K$ for more than one temperature is given, the difference may be several tenths of a unit.

The *pressure* dependence of an equilibrium constant is given by the formula $(\delta \log K/\delta p)_T = -\Delta V/(RT \ln 10)$. At 5°C, the change in $\log K$ would be approximately $-1.9 \times 10^{-5} p\Delta V$, with p in atmospheres and ΔV in milliliters. For example, for the reaction $CaCO_3\ (s) \rightleftharpoons Ca^{++} + CO_3^{--}$, $\Delta V \sim -50$ ml, and so $\log K$ would increase by about 0.2 unit at the average pressure (200 atm), and by about 0.4 unit at the average depth of the ocean floor. However, many other equilibria, such as the dissociation equilibria of H_2CO_3, will also change with pressure with comparable amounts. No attempt has been made to correct for such variations.

The following treatment of the equilibria may horrify some physical chemists; certainly, it is not as strict as would be required in treating equilibria in a laboratory. However, considering the many uncertain factors, it does not seem worth while to strive for greater accuracy in those isolated points where it could be achieved. The present treatment may be adequate for the purpose, which is to provide a basis for discussing the main species present in the solution, and the solid phases that determine the composition of the solution.

Major Constituents

Water and Silica

In mixing our ocean model, we start with 54.90 mole H_2O. The elements will usually be added as hydroxides, or oxides. Since H_2O is present in great excess, we shall not be very particular about counting the O and H atoms.

First, we add 6.06 mole SiO_2. At equilibrium, it would be present as solid quartz, SiO_2, an important constituent of marine sediments. The solubility of quartz in water has been given as $10^{-3.74}M$ at 25°C ($10^{-4.10}M$ at 0°C) (Van Lier, 1959). The Si is likely to exist mainly as mononuclear units $Si(OH)_4$ and not as a colloid as was believed earlier.

For the bottom water of the ocean, figures from 1000 mg Si/m^3 (Atlantic) to 3000 (Antarctic) have been given, which would correspond to $10^{-4.5}$ to $10^{-4.0}M$. In the upper layers, much lower concentrations (below $10^{-6}M$) have been observed, which is ascribed to the action of diatoms.

The acidity constants of $Si(OH)_4$ in $0.5M$ NaCl at 25°C are $10^{-9.41}$ and $10^{-12.71}$ (Ingri, 1959). At the pH of the ocean, only about 5 per cent of the Si would then exist as $SiO(OH)_3^-$, or $H_3SiO_4^-$.

Aluminum

We return to our imaginary experiment, and add 1.85 mole $Al(OH)_3$ to the mixture. At real equilibrium there would now be two solid phases: one is quartz SiO_2, and the other is probably kaolinite, $Al_2Si_2O_5(OH)_4$. In the solution, the equilibrium concentration of $Si(OH)_4$ will be unchanged, since we have quartz in excess, as always in the following.

Unfortunately, it is hard to say what the dissolved aluminum species will be. At somewhat higher acidities, aluminum is known to form unexpectedly large complexes. For instance, discrete groups $Al_{13}O_{40}H_{48}^{7+}$ have been found in crystal structures (Johansson, 1960; Johansson *et al.*, 1960), and similar complexes are also likely to exist in solution (G. Biedermann, unpublished). The concentrations of Al in sea water reported earlier range from approximately $10^{-4.0}$ to $10^{-6.7}M$. According to Sackett and Arrehnius (1959) the concentration of dissolved Al is only between $10^{-7.7}$ and $10^{-7.0}M$. We shall have to leave open the question of whether Al exists mainly as an aluminum polyion, or as a mononuclear species, like $Al(OH)_2^+$ or $Al(OH)_3$. The hydrolysis of aluminum is under active investigation in Stockholm, and we may know more in a decade or so. At any rate, this soluble aluminum species must play an important role in the building up of various silicate minerals.

Chloride and Main Cations

Next come seven elements in amounts of the same order of magnitude, between 0.41 and 0.76 mole/liter sea water. Let us set aside the iron for a time, to be added later, and also the carbon, in the form of 0.46 mole $CaCO_3$ and 0.09 mole $MgCO_3$. Thus, we add to our equilibrium mixture 0.55 mole HCl, 0.76 mole NaOH, 0.41 mole KOH, 0.44 mole MgO, and 0.10 mole CaO. This will lead to a rearrangement of part of the solids. Whereas an excess of quartz still remains, part of the quartz and perhaps all the kaolinite is rearranged to aluminosilicates with a charged aluminosilicate framework, in which Mg may have replaced some Al and Na^+, K^+, Mg^{++}, and Ca^{++} may have entered the holes of the framework. Glauconite is an example of an aluminosilicate with a layer structure. It is abundant in marine sediments and belongs to the mica group of the clay minerals. For glauconite the average formula $K_{0.62}Na_{0.09}Ca_{0.06}Mg_{0.40}Fe_{1.16}Al_{0.82}Si_{3.65}O_{10}(OH)_2$ has been given (Jasmund, 1955, p. 154). An abundant aluminosilicate with a zeolite structure is phillipsite, which may be written as $(M'Si,M''Al)AlSi_2O_8(H_2O)_3$, with $M' = Na$ or K, $M'' = Ca$ or Ba.

Although numerous studies have been made on the ion exchange on single silicate minerals, as yet too little seems to be known about their relative stabilities to answer the question as to what the real equilibrium will be after the additions mentioned. One may predict that the solids will contain quartz, and at least two more phases. Because of the wide occurrence of micas like glauconite, and of phillipsite, one may guess that they would correspond to a real equilibrium state. The solution, on the other hand, will contain the chloride ions, Cl^-, which cannot leave it, and, moreover, a sufficient number of positive ions to correspond to the negative charge of $0.55M$ Cl^-. The result will be, loosely speaking, an ion exchange equilibrium of the positive ions between the solution and the silicate phases.

As a schematic example of the type of equilibria involved, one may take a reaction:

$$3Al_2Si_2O_5(OH)_4\ (s) + 4SiO_2\ (s) + 2K^+ + 2Ca^{++} + 9H_2O \rightleftharpoons 2KCaAl_3Si_5O_{16}(H_2O)_6\ (s) + 6H^+$$

$$\log K = 6 \log [H^+] - 2 \log [K^+] - 2 \log [Ca^{++}]$$

In addition, there will be ion exchange equilibria between the solution and each separate phase. The experimental fact that K^+ is bound more strongly than Na^+ to layer silicates is reflected in the ratios $(Na/K)_{\text{solid}} = 10^{-0.14}$, $(Na/K)_{\text{solution}} = 10^{1.67}$ in sea water. Similarly, Ca^{++} is bound more strongly than Mg^{++}, so that there will be a concentration of Na^+ and Mg^{++} in the sea water.

A very important point is that these equilibria are pH-dependent (see the equation above). Indeed, here we seem to have the main buffering factor in the ocean. May I suggest that, when the equilibrium relationships solution/silicate minerals are better understood, it will be found that the pH of the ocean, 8.1, is practically determined by the ratios of the constituents we have considered up till now, and that the addition of the following constituents will change pH only by, say, 0.1 or 0.2 unit. The greatest change will perhaps be that on addition of FeOOH.

Carbonate

Now let us add 0.46 mole $CaCO_3$ and 0.09 mole $MgCO_3$. As a first approach to equilibrium these form 0.09 mole dolomite, $MgCa(CO_3)_2$, and 0.37 mole calcite, $CaCO_3$. Some $MgCO_3$ would also go into solid solution in the calcite phase. The question is controversial whether average sea water would be at equilibrium with a mixture of calcite and dolomite,

$$2CaCO_3\ (s) + Mg^{++} \rightleftharpoons CaMg(CO_3)_2\ (s) + Ca^{++}$$

whether it would tend to transform calcite to dolomite, or the other way round. The experimental data are contradictory, the equilibrium is probably pressure-dependent, and we shall avoid the question by again setting aside the dolomite; this does not change the remainder of our argument.

Thus, leaving out the dolomite, we add 0.37 mole $CaCO_3$ to our mixture. At equilibrium, a small part of the calcite will have dissolved. In Table III are given equilibrium constants for infinite dilution (zero activities), and for sea water, which is an artificial sea water of 35 per cent salinity, close to our average sea water; the latter figures are from Buch (quoted by Harvey, 1957) and Kramer (1958, 1959).*

TABLE III. Approximate Equilibrium Constants

Reaction	Sea Water		Infinite Dilution	
	5°C	25°C	5°C	25°C
$CaCO_3\ (s) \rightleftharpoons Ca^{++} + CO_3^{--}$	−5.67	−6.19	−8.20	−8.32
$CO_3^{--} + H^+ \rightleftharpoons HCO_3^{3-}$	9.18	8.96	10.56	10.33
$HCO_3^- + H^+ \rightleftharpoons H_2CO_3$	6.15	5.99	6.52	6.36
$H_2CO_3 \rightleftharpoons CO_2\ (g) + H_2O$	1.27	1.53	1.19	1.47
$CaCO_3\ (s) + H^+ \rightleftharpoons Ca^{++} + HCO_3^-$	3.51	2.77	2.36	2.01
$\log [HCO_3^-]$	−2.60	−3.34	−3.75	−4.10

The values for $\log [HCO_3^-]$ have been calculated from $\log [Ca^{++}] = -1.99$, and pH = 8.1, both of which are determined by the equilibria solution/silicates, according to the argument above.

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* Neither set of figures is as accurate as one may have wished. Kramer (1959) changed his first value (1958) for $\log K_s(CaCO_3)$ by −0.12; and equal correction is made here on his first value (1958) for 5°C. The "infinite dilution" figures are estimates on the basis of not too concordant literature data and positively are not claimed to be critically deduced "best" values. However, the figures in Table III may indicate the influence of temperature and ionic medium, and the approximate $[HCO_3^-]$ and P_{CO_2} to be expected at equilibrium.

Actually, log $[HCO_3^-]$ = -2.63 in sea water, which indicates that it would not be far from equilibrium with $CaCO_3$ at some temperature around 5°C, which is in the neighborhood of the average temperature, especially close to the bottom of the ocean.

When water from deeper levels approaches the surface, the pressure is decreased and the temperature usually increased. For both reasons, the water becomes supersaturated with $CaCO_3$. However, we shall not step aside to discuss the transport phenomena involved but pursue our imaginary equilibrium experiment.*

By applying the equilibrium constants given above, and the known pH and $[Ca^{++}]$, we calculate log $[H_2CO_3]$ = -4.55; log $[CO_3^{--}]$ = -3.68; log p_{CO_2} = -3.28. The value for log p_{CO_2} agrees rather well with the average value for the atmosphere, around -3.52, considering the uncertainties involved in the calculation.

It may be noted that if the equilibria are considered this way, the carbonate system becomes only an indicator for the pH, whereas pH is really determined by the silicates. If there had been no carbonate in the solution, the role of the indicator would have been taken over by the next available acid-base pair, borate or even dissolved silicate.

Let us suppose that we release rather suddenly a large amount of CO_2—for instance, that we double the amount of CO_2 in the gas phase, which is by now about 0.04 mM/liter sea water. This might, for the next few decades, mean a measurable decrease in the pH of the surface water of the ocean, perhaps by as much as 0.2 unit. However, the processes would start to work toward equilibrium: the H_2CO_3 would spread out over the whole bulk of the ocean, $CaCO_3$ would dissolve, and there would be a readjustment of the silicate equilibria. Considering the enormous buffering capacity of the silicates—of the order of 1 mole/liter sea water in comparison with 0.00004 mole CO_2—the final change would probably not be perceptibly different from the initial one.

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* The solubility increases exponentially with pressure (its logarithm increases linearly). A detailed study of the equilibria and kinetics involved would probably explain the abrupt decrease of $CaCO_3$ content in sediments at depths around 4500–5000 m, described in Dr. Bramlette's paper (p. 345).

Oxygen: pE

Now that pH is determined, we shall add 0.027 mole O_2, which will mainly stay in the gas phase. Some will, however, dissolve in the water (concentration of the order of $0.0002M$), and will be important for maintaining the oxidation potential, which is conveniently expressed by means of the quantity pE, which is a measure of the electron activity in a solution, in analogy to pH which measures its proton activity.

$$\mathrm{pE} = -\log\{e^-\}, \quad \mathrm{pH} = -\log\{\mathrm{H}^+\}$$

To obtain pE, divide the oxidation potential of a solution (on the hydrogen scale) by the factor $RTF^{-1}\ln 10$, which is 0.05915 v (25°C), 0.05419 v (0°C). In sea water, as in our equilibrium mixture, pE is determined by the equilibrium with atmospheric oxygen (25°C, zero activity):

$$\tfrac{1}{2}\mathrm{O_2\,(g)} + 2\mathrm{H}^+ + 2e^- \rightleftharpoons \mathrm{H_2O}, \quad \log K = 41.55$$

$$\begin{aligned}\log K &= \log\{\mathrm{H_2O}\} - \tfrac{1}{2}\log p_{\mathrm{O}_2} - 2\log\{\mathrm{H}^+\} - 2\log\{e^-\}\\ &= -0.01 - \tfrac{1}{2}\log 0.21 + 2\mathrm{pH} + 2\mathrm{pE}\\ &= -0.01 + 0.34 + 16.4 + 2\mathrm{pE}\\ \mathrm{pE} &= \tfrac{1}{2}(25.0) = 12.5\end{aligned}$$

This value for pE is not very sensitive to the usual small variations of pH and oxygen concentration. A change of pH with ±0.1 unit will change pE by ±0.1. A deficiency of oxygen will decrease pE, but in order to lower pE by 0.1 unit, one has to lower the oxygen content to $10^{-0.4}$ or 40 per cent of the saturation value.

Iron

We now add 0.55 mole iron to our mixture, mainly in the form of FeOOH (strictly speaking, a certain percentage should be added as FeO). At equilibrium, some iron will have reacted with the silicate phases, but a considerable part will remain as FeOOH. The amount of the silicate phases will have increased, and they will contain some Fe^{3+} in Al^{3+} positions, and perhaps some Fe^{++} in Mg^{++} positions. This adjustment will probably cause some slight change in the pH, and it might have been more logical to add the iron before the $CaCO_3$.

Sea water contains some iron in true solution. The analyses vary from $10^{-7.9}$ to $10^{-6.0}M$, but for carefully filtered samples $10^{-7.2}$ seems to be a good average (Lewis and Goldberg, 1954). It is natural to ask what soluble iron species can be present. The first guess is that it is perhaps some hydroxo complex of iron(III). For $3M$ $NaClO_4$, 25°C (Biedermann and Schindler, 1957; Hedström, 1953):

Reaction	log K
$FeOOH\ (s) + 3H^+ \rightleftharpoons Fe^{3+} + 2H_2O$	3.96
$Fe^{3+} + H_2O \rightleftharpoons FeOH^{++} + H^+$	−3.05
$FeOH^{++} + H_2O \rightleftharpoons Fe(OH)_2^+ + H^+$	−3.26
$2Fe^{3+} + 2H_2O \rightleftharpoons Fe_2(OH)_2^{4+} + 2H^+$	−2.91

It is easily seen that the most important reaction will be

$$FeOOH\ (s) + H^+ \rightleftharpoons Fe(OH)_2^+ + H_2O, \quad \log K = -2.35$$

which will give, with pH = 8.1, $[Fe(OH)_2^+] = 10^{-10.45}$. For $FeOH^{++}$ and $Fe_2(OH)_2^{4+}$, we find concentrations of the order of 10^{-15} and 10^{-27}. Even if the formation constant for $Fe(OH)_2^+$ is the most uncertain of those given, it is not likely to be too small; nor should equilibrium be very sensitive to a change in ionic medium. The discrepancy between the equilibrium concentration of the $Fe(OH)_2^+$, $10^{-10.45}$, and the observed iron concentration, around $10^{-7.2}$, seems too great to be explained by activity factors, or by any temperature influence on the equilibria.

The concentration of Fe^{++} may be estimated from the equilibria:

Reaction	log K
$FeOOH\ (s) + 3H^+ \rightleftharpoons Fe^{3+} + 2H_2O$	4.0
$Fe^{3+} + e^- \rightleftharpoons Fe^{++}$	13.0
$FeOOH\ (s) + 3H^+ + e^- \rightleftharpoons Fe^{++} + 2H_2O$	17

Then:

$$\log [Fe^{++}] = 17 - 3pH - pE = 17 - 24.3 - 12.5 = -20$$

We have been somewhat careless with the activity coefficients in these formulas but it is obvious that the equilibrium concentration of Fe^{++} cannot explain the observed iron concentration in sea water.

Probably some iron species exist in sea water other than those we have considered. One might think of the organic matter present, which certainly does not represent an ultimate equilibrium state but still may form rather stable complexes in water. Concentrations of organic carbon have been given ranging from 0.14 to 2.72 mg C/liter, thus from $10^{-4.9}$ to $10^{-3.6}M$. It is conceivable that this carbon is partly in the form of some strong and relatively stable complex former. However, until something definite is known about these organic substances, one should look out for other possible forms of iron. One possibility is indicated in recent work by Lengweiler (1959), who studied the solubility of FeOOH at various pH and found a pH-independent term of about $10^{-7}M$, which may correspond to uncharged $Fe(OH)_3$ or a polymer of it. This may be the species we have in sea water. We may note that Lewis and Goldberg (1954) reported a practically constant concentration of "soluble iron" as distinguished from "particulate iron" of $10^{-7.2}M$.

It is desirable to have the solubilities of a series of hydroxides and oxides in water studied by some method, such as radioactive tracers, that would allow one to measure concentrations a few powers of ten lower than those usually studied. It seems very likely that one would then find evidence for uncharged species, like the previously known $Si(OH)_4$ and $Hg(OH)_2$. It is also possible that such species would be the prevalent form of several elements in the ocean.

Whereas fluoride, chloride, or sulfate complexing of iron(III) do not seem able to compete with hydroxo complexing, too little is known about phosphate complexing to exclude it.

Titanium

Next addition to our equilibrium mixture is 0.06 mole of TiO_2. At equilibrium, some Ti may have entered the silicate phases by substitution, and the rest remained as TiO_2 (s), probably rutile. There seems to be no laboratory evidence of any soluble species that one could expect to find at the conditions of sea water; the analyses of up to $10^{-6.7}M$ in sea water may refer to uncharged $Ti(OH)_4$.

Fluoride

Next we add 0.03 mole HF. At equilibrium, some of the fluoride may enter the silicate phases, substituting O^{--} or OH^- groups; at present it is impossible to predict where these equilibria will stand. It is conceivable that some of the fluoride might precipitate as CaF_2 (s), fluorspar. For the reaction

$$CaF_2\ (s) \rightleftharpoons Ca^{++} + 2F^-, \quad \log K = \log\ [Ca^{++}] + 2\log\ [F^-] + \log f_2 f_1^2$$

zero activity values of about -10.7 at 0°C, and -10.4 at 25°C have been given. With $\log\ [Ca^{++}] = -2.0$, and estimating $\log f_2 f_1^2 = -1.2$, we find $\log\ [F^-] = -3.75\ (0°), -3.6\ (25°)$ at equilibrium with solid CaF_2.

Of the ions in the solution, it seems that only Mg^{++} would form considerable amounts of fluoride complexes. For the comparable medium $0.5M$ $NaClO_4$, Connick and Tsao (1954) give

$$Mg^{++} + F^- \rightleftharpoons MgF^+, \quad \log K = 1.30\ (25°), \quad 1.20\ (15°)$$

Since $\log\ [Mg^{++}] = -1.27$, we would expect to have, in addition to the $10^{-3.75}$ to $10^{-3.6}M$ of F^-, an approximately equal concentration of MgF^+, giving a total F concentration of $10^{-3.5}$ to $10^{-3.3}$. This is higher than the concentration found in sea water, $10^{-4.15}M$, so it may not be worth while to look out for fluorspar in marine sediments. Probably most of the F is in silicate phases and some in the apatite (see below).

Sulfate

The addition of 0.03 mole H_2SO_4 will allow a larger amount of ions in the solution and cause some rearrangement in the silicate phases. Considering the great amount of silicates present, we do not expect any perceptible change in the equilibrium pH. (Those who are very cautious might have saved some Na and added sulfur as Na_2SO_4 at this point.)

One may now ask whether the conditions are such that calcium sulfate will precipitate. For the reaction

$$CaSO_4(H_2O)_2\ (s) \rightleftharpoons Ca^{++} + SO_4^{--} + 2H_2O$$

the zero activity product is $10^{-4.63}$ (25°). From available data on the solubility of $CaSO_4\ (H_2O)_2$ in NaCl and $NaClO_4$ solutions, one would estimate for sea water a concentration solubility product of $10^{-2.9}$, which would vary rather little with temperature.

In average sea water we have $[Ca^{++}][SO_4^{--}] = 10^{-3.54}$, which indicates that no solid $CaSO_4(H_2O)_2$ will be present at equilibrium. The sulfate found in some marine sediments is probably adsorbed to the phases previously mentioned.

Sulfate ions seem to form complexes with bivalent metal ions:

$$M^{++} + SO_4^{--} \rightleftharpoons MSO_4$$

with zero activity constants that are approximately equal, around $10^{2.2}$ at 25°C for most bivalent cations. In the ionic medium of sea water, the stability constant should be considerably less, perhaps of the order of $10^{0.5}$. At any rate, a minor part of Ca^{++} and Mg^{++} will be present as uncharged complexes, $CaSO_4$ and $MgSO_4$ in solution.

Phosphate

Next addition is 0.02 mole H_3PO_4, or Na_2HPO_4, if we want a minimum rearrangement in the silicate phases. At the final equilibrium, we may expect much of the phosphate to be precipitated in the form of some calcium phosphate. The literature data on the solubility of calcium phosphates do not agree as well as one could wish: there are difficulties in getting true equilibria, and identifying the phases. The following estimates (25°C, zero activities) are based on data of Farr (1950), Kauko and Eyubi (1955):

$$CaHPO_4\ (s) \rightleftharpoons Ca^{++} + HPO_4^{--}, \quad \log K = -7.0$$

$$Ca_3(PO_4)_2\ (s) \rightleftharpoons 3Ca^{++} + 2PO_4^{3-}, \quad \log K = -26.0$$

$$Ca_5(PO_4)_3OH\ (s) \rightleftharpoons 5Ca^{++} + 3PO_4^{3-} + OH^-, \ \log K = -55.9$$

In adding

$$HPO_4^{--} \rightleftharpoons PO_4^{3-} + H^+, \quad \log K = -12.3$$

$$H_2O \rightleftharpoons H^+ + OH^-, \quad \log K = -14.0$$

we find

$$3CaHPO_4\ (s) + 2Ca^{++} + H_2O \rightleftharpoons Ca_5(PO_4)_3OH\ (s) + 4H^+, \ \log K = -16$$

$$3Ca_3(PO_4)_2\ (s) + Ca^{++} + 2H_2O \rightleftharpoons 2Ca_5(PO_4)_3OH\ (s) + 2H^+, \quad \log K = \quad 6$$

Thus, at equilibrium between the first two calcium phosphate phases, we would have $2 \log \{H^+\} - \log \{Ca^{++}\} = -8$; in the second equilibrium, the difference would be 6. In sea water, we have $2 \log \{H^+\} - \log \{Ca^{++}\} = -16.2 + 2.8 = -13.4$. It seems that no reasonable error in the experiments quoted, activity, pressure, or temperature correction, would change the fact that the two last reactions given would proceed completely to the right, under the conditions of sea water, so that $Ca_5(PO_4)_3OH$ (s), hydroxyapatite, would be the only stable calcium phosphate phase. This agrees with experience on oceanic sediments, I have learned. The important equilibrium will then be, since phosphate exists mainly as HPO_4^{--}

$$Ca_5(PO_4)_3OH\ (s) + 4H^+ = 5Ca^{++} + 3HPO_4^{--} + H_2O, \quad \log K = -5.0$$

Inserting pH $= 8.1$, $\log [Ca^{++}] = -2.0$, and estimating $\log f_2 = -0.8$ we find $\log [HPO_4^{--}] = -7.0$.

This is admittedly a very rough estimate; for instance, the influence of temperature on the equilibria could not be considered. The total amount of P in the equilibrium solution should be larger, because in addition to $10^{-7.0}M$ free HPO_4^{--} there will be complexes of this ion with Mg^{++} and Ca^{++}, which are slightly stronger than the sulfate complex.

The total P concentration found in deep sea water, $30 - 90$ mg/m^3 $= 10^{-6.0}$ to $10^{-5.5}M$, together with this very approximate calculation, would indicate that the lower layers may be at equilibrium with hydroxyapatite; in the upper layers, as well known, the P content is decreased locally by organic activity.

Phosphate ions are said to be adsorbed on FeOOH and, to some extent, on the silicate phases. Unfortunately, very little is known about the solubility equilibria of various phosphates, such as $FePO_4$. In the scanty measurements that exist it seems that the solubility equilibrium has not been kept distinguished from complex formation and hydrolysis equilibria. More work on phosphate equilibria would be desirable. At present it cannot be said if any more phosphate, such as $FePO_4$, could exist at equilibrium as a separate solid phase.

Manganese

Now we add the last of our major elements, 0.01 mole Mn in the form of MnO_2. From the equilibrium constants, and the pE and pH of sea water, it is easily found that MnO_2 is the only manganese oxide phase that would be stable.* One also finds that of the soluble species that have been studied, Mn^{++} and MnO_4^- would be the most important ones, though their concentrations at equilibrium will be small indeed:

$$MnO_2\,(s) + 4H^+ + 2e^- \rightleftharpoons Mn^{++} + 2H_2O, \quad \log K = 41.6$$

$$\log \{Mn^{++}\} = 41.6 - 4pH - 2pE = 41.6 - 32.4 - 25.0 = -16$$

$$MnO_4^- + 4H^+ + 3e^- \rightleftharpoons MnO_2\,(s) + 2H_2O, \quad \log K = 86.0$$

$$\log \{MnO_4^-\} = -86.0 + 4pH + 3pE = 32.4 + 37.5 - 86.0 = -16$$

The total concentrations of manganese actually reported are between $10^{-6.7}$ and $10^{-7.9}M$. It seems dubious that Mn^{++} or MnO_4^- could exist for long periods at concentrations some 10^9 times the equilibrium value.

If one does not prefer some unknown organic or phosphate complex as a *deus ex machina*, the best guess is perhaps some uncharged hydroxide species, such as $Mn(OH)_3$ or $Mn(OH)_4$.

Nitrogen

In our equilibrium mixture, to be strict, we have also around 0.10 mole N_2, chiefly present as N_2 in the air. This is an outrageous case of nonequilibrium. The N_2 molecule is certainly inert, and whatever lightning is doing to approach equilibrium by forming nitrite and nitrate, this is counteracted by biological activity. We shall leave N out of the discussion, except to remind us for a moment that there are limitations to the equilibrium treatment.

It would have little relation to present conditions to calculate what the equilibrium with N would be. On the other hand, the present concentrations of NH_3 and NO_3^- in the ocean are so small

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* In deep sea sediments, indeed, δ-MnO_2 is an abundant constituent. There is also a "manganite" phase (or perhaps two) described by Dr. Buser. It may be described as a solid solution phase containing MnO_2 and oxides of various bipositive metals. If it exists at equilibrium with MnO_2, as it seems to do, its presence would make no change in the discussion of the dissolved Mn species.

that they do not seem to influence the inorganic equilibria; for instance, the ammonia complexes cannot compete with the hydroxide or chloride complexes.

Minor Constituents

We have discussed the seventeen constituents that exist in more than 0.01 mole in our equilibrium mixture: 1 liter of model ocean water and its share of atmosphere and sediments.

Table IV gives the negative logarithms of the number of moles of each element in the sediments (*n* mole/liter sea water) and in solution (*c* mole/liter); again, *n* is calculated from Goldschmidt's estimates. An attempt has been made, for many elements, to state which species is likely to be predominant in the solution, and which solid phase, if any, is likely to determine its concentration. These formulas are often rather uncertain, because of the limited amount of data available; however, they have been set down as the best guess the present author could make, and as a start for a discussion.

Table IV begins with the major constituents; for them it summarizes the results of the preceding section. The minor constituents are then given in groups, in the order of decreasing abundance; within each group, the order is that of increasing atomic number.

Let us suppose that all the minor elements are added at once to our model ocean, as hydroxides, oxides, or chlorides, and discuss the final equilibrium that will result. No attempt will be made at a comprehensive treatment of the minor elements; certain general points will be made, however, and the equilibria of a few elements will be discussed in detail.

Solid Solutions

The naturally occurring solid phases are very seldom pure substances but rather solid solutions, in which some elements have been replaced to a greater or less extent by other elements that would fit into the crystal structure. Notable examples are the silicate phases already mentioned. In our model ocean equilibrium mixture, most of the phases (with the possible exception of SiO_2) will to an appreciable degree be solid solutions.

TABLE IV. Amounts of Various Elements per Liter Average Sea Water[a]

Element	$-\log n_{\text{solid}}$	$-\log c_{\text{sol.}}$	Main Dissolved Species	Solid Phase
H_2O	—	−1.74	H_2O	
Si	−0.78	4.0–4.5	$Si(OH)_4$	SiO_2
Al	−0.27	7.0–7.7	$Al(OH)_3$?	$Al_2Si_2O_5(OH)_4$[b]
Cl		0.26	Cl^-	—
Na	0.54	0.33	Na^+	Silicates, pH = 8.1
Ca	0.26	1.99	Ca^{++}	
Mg	0.32	1.27	Mg^{++}	
K	0.40	2.00	K^+	
C	0.26	2.63	HCO_3^-	$CaCO_3$, $CaMg(CO_3)_2$
O_2	—	(1.57, g)	(O_2, g)	pE = 12.5
Fe	0.26	6.0–7.9; 7.2	$Fe(OH)_3$?	FeOOH
Ti	1.25	6.7>8	$Ti(OH)_4$?	TiO_2
F	1.54	4.15	F^-, MgF^+	—
S	1.4	1.55	SO_4^{--}	—
P	1.63	5.5–6.0	HPO_4^{--}	$Ca_5(PO_4)_3OH$
Mn	1.95	6.7–7.9	$Mn(OH)_{3,4}$?	MnO_2
N_2	—	(1.00, g)	(N_2, g)	
Li	2.24	4.3·5.0	Li^+	
B	1.5	3.37	$B(OH)_3$	
V	2.7	6.9–8.4	$VO_2(OH)_3^{--}$	
Cr	2.6	7.3–9.1	(OH)?	
Zn	2.9	6.5–7.7	${}^{+}Zn$	
Rb	2.7	5.3–6.4	Rb^+	
Sr	2.7	3.82	Sr^{++}	$SrCO_3$
Zr	2.8	+	(OH)?	
Ba	3.0	6.2–7.4	Ba^{++}	$BaSO_4$
Be	3.4	?	(OH)?	
Co	3.6	7.9–8.8	Co^{++}	CoOOH
Ni	3.1	7.0–8.9	Ni^{++}	
Cu	3.2	5.8–8.4	Cu^{++}, $CuOH^+$	$Cu(OH)_{1.5}Cl_{0.5}$?
Ga	3.9	8.1	(OH)?	
Br	?	3.08	Br^-	—
Y	3.7	8.5	(OH)?	YPO_4?
Sn	3.7	7.6	(OH)?	SnO_2?
Ce	3.7	8.5	Ce^{3+}?	CeO_2?

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[a] n moles in sediments; c moles in solution. *Tentative* formulas for main dissolved species, and solids at equilibrium are given. Many elements may, at equilibrium, form not a separate solid phase but solid solutions with compounds of more abundant elements. This may be true also where a formula for a solid is given (CoOOH may dissolve in FeOOH, PbO_2 in MnO_2, see text).

[b] May disappear on adding following elements.

TABLE IV. (*Continued*)

Element	$-\log n_{\text{solid}}$	$-\log c_{\text{sol.}}$	Main Dissolved Species	Solid Phase
Sc	4.2	9	(OH)?	$ScPO_4$?
Ge	4.2	>8.9	$Ge(OH)_4$	
As	4.4	6.4–7.5	$HAsO_4^{--}$	
Mo	4.0	6.8–8.5	MoO_4^{--}	
Cs	4.5	7.1–8.5	Cs^+	
La	4.1	8.7	La^{3+}, $LaOH^{++}$?	$LaPO_4$?
Pb	4.3	7.6–8.0	Pb^{++}, $PbOH^+$, $PbCl^+$	PbO_2
Th	4.5	>8	(OH)?	
Sb	5.3?	>8.4	$Sb(OH)_6^-$?	
I	6?	6.3–6.7	IO_3^-	
W	5?	9.3	WO_4^{--}	
Hg	5.8	9.8	$HgCl_4^{--}$	
Tl	5–6	>10.3	Tl^+	
U	5.0	7.9–9.2	$UO_2(CO_3)_3^{4-}$?	
Se	6.2	7.1–7.4	SeO_4^{--}	
Ag	6.2	7.6–8.9	$AgCl_3^{--}$	
Cd	6.1	9.3–9.5	$CdCl_2$?	
Bi	6.2	9	?	
Au	7.8	8–10.7	$AuCl_2^-$	

In the literature there are a few accurate studies of the equilibria between aqueous and solid solutions, especially Vaslow and Boyd (1952) on Ag(Cl, Br) and Schmeling (1953) on (Ba, Sr)CO_3. On the important silicate equilibria so little is known that there is practically no basis for a strict treatment in our present discussion.

Let us consider a schematic case, without attempting to use any actual values: a solid solution (A,B)L, say (Ca, Sr)CO_3, which may be described as solid AL, where part of the A ions have been replaced by B. Let the mole fractions be x_A and x_B so that $x_A + x_B = 1$. Let us suppose that the solid solution is ideal. Deviations from ideality will not change the following argument. Then the activity of each component is equal to its mole fraction. The conditions for equilibrium with an aqueous solution would be (omitting the charges):

$$\{A\}\{L\} = x_A K_{AL}; \quad \{B\}\{L\} = x_B K_{BL}$$

Hence, K_{AL} and K_{BL} are the solubility products of pure AL and pure BL (with the AL structure).

If the activity coefficients are canceled out, we would have

$$\frac{[B]}{[A]} = \frac{x_B}{x_A} \cdot \frac{K_{BL}}{K_{AL}} = \frac{n_B}{n_A} \cdot \frac{K_{BL}}{K_{AL}}$$

The equations show that B may precipitate with AL, to some extent, although the product of the B and L activities is much lower than K_{BL}. The ratio B/A will be higher in the solid phase than in the solution, if BL is less soluble than AL. If solid solutions are formed, the effect is as if the B were extracted by the AL: the more AL (n_A moles) present, the more B (n_B moles) will be in the solid phase.

In our equilibrium mixture, as in actual sea water, many of the minor constituents may disappear almost completely into solid solutions with the phases formed by the major constituents, instead of forming a separate phase at equilibrium.

Complex formation

At the pH of sea water, *hydroxide* complexing is important for all ions of oxidation number greater than 2. The *chloride* complexing has to compete with the hydroxide. For a certain metal ion, M (omitting the charge), let $K_{Cl} = [MCl]/[M][Cl^-]$, and $K_{OH} = [MOH]/[M][OH^-]$. It is easily seen that for MCl to predominate over MOH, it is necessary that

$$\log K_{Cl} - \log K_{OH} > \log [OH^-] - \log [Cl^-] \approx -5.4$$

A study of available complex formation constants shows that this is true only for a few ions, grouped in the middle of the periodic system: Ag^+, Hg^{++}, perhaps Cd^{++} and Pb^{++}. These are likely to exist predominantly as complexes: $AgCl_2^-$, $AgCl_3^{--}$, $HgCl_3^-$, $HgCl_4^{--}$. To this group also belongs $AuCl_2^-$. However, we shall see that for gold(III), the hydroxo complexes predominate.

Similarly, for the *fluoride* complexes to predominate over the hydroxo complexes we would have

$$\log K_F - \log K_{OH} > \log [OH] - \log [F^-] \approx -1.5$$

This requirement is fulfilled for Mg^{++}, for which $\log K_{OH} \approx 2.1$, $\log K_F \approx 1.3$, and thus neither is very strong. Otherwise, there seems to be no certain case of predominant fluoride complexing.

Sulfate complexes may be formed by a number of bipositive ions with weak OH complexing, like Mg^{++}, Co^{++}, with stability constants around $10^{0.5}$ (see above), which would mean that (with $10^{-1.5}M$ SO_4^{--}), something like 5 to 10% of the metal would be sulfato complexes. With ions of higher charge, the tendency to sulfate complexing increases, but so does the hydroxide complexing. I am aware of no ion of which it can be said with certainty that it exists chiefly as sulfate complexes, under the conditions of sea water.

Carbonate complexes have been studied for several cations such as UO_2^{++} and Th^{4+}. *Phosphate* complexes are known to exist, in more acidic solution, with Fe^{3+}, Al^{3+}, UO_2^{++} and many others. The available data do not seem to allow any certain conclusion as to the extent of carbonate and phosphate complexing in our equilibrium mixture.

Finally, there remain our unknown *organic compounds*, of concentration 10^{-5} to $10^{-4}M$, which may or may not be strong complex formers with some of the metal ions. Like HPO_4^{--} and CO_3^{--}, the organic complexes might give the main contribution to some of the elements present at very low concentrations, say 10^{-6} or $10^{-7}M$, whereas their complexing with the major constituents would not change the equilibria very much.

Some Anion Redox Equilibria

Halogens and S. A check on the redox equilibria of Cl, Br, and S shows, as might be expected, that the predominating species, at the pE and pH of the ocean, must be Cl^-, Br^-, and SO_4^{--} at equilibrium. For instance, we have

$$ClO_3^- + 6H^+ + 6e^- \rightleftharpoons Cl^- + 3H_2O, \qquad \log K = 147.2$$

$$BrO_3^- + 6H^+ + 6e^- \rightleftharpoons Br^- + 3H_2O, \qquad \log K = 146.3$$

$$IO_3^- + 6H^+ + 6e^- \rightleftharpoons I^- + 3H_2O, \qquad \log K = 110.1$$

By inserting $pE = 12.5$, $pH = 8.1$, we find the ratios $[ClO_3^-]/[Cl^-] \approx [BrO_3^-]/[Br^-] \approx 10^{-23}$, but $[IO_3^-]/[I^-] = 10^{13.5}$. Thus, whereas Cl^- and Br^- predominate, it seems that at equilibrium IO_3^- would be much more important species than I^- in sea water. Calculations show that also HIO, IO^-, ICl_2^-, ICl, ICl_3, IBr_2^-, periodate, and I_2 are negligible in comparison with IO_3^- at equilibrium.

Some authors have given experimental evidence that sea water would contain a certain proportion of the iodine as I^- ions. This may be so because of nonequilibrium. However, it may be pointed out that it is hard to make such an experimental proof that is not open to criticism; for instance, IO_3^- may well coprecipitate with AgCl, just as does I^-.

Arsenic. At pH = 8.1, arsenic(III) will exist mainly as the uncharged species, say $HAsO_2$ [though $As(OH)_3$ might be more nearly correct], and arsenic(V) as the ion $HAsO_4^{--}$. We combine the equilibria

$$\begin{array}{lll} AsO_4^{3-} + 2H_2O + 2e^- \rightleftharpoons AsO_2^- + 4OH^-, & \log K = & -22.7 \\ H^+ + AsO_2^- \rightleftharpoons HAsO_2, & \log K = & 9.1 \\ HAsO_4^{--} \rightleftharpoons AsO_4^{3-} + H^+, & \log K = & -11.5 \\ 4H^+ + 4OH^- \rightleftharpoons 4H_2O, & \log K = & 56.0 \\ \hline HAsO_4^{--} + 4H^+ + 2e^- \rightleftharpoons HAsO_2 + 2H_2O, & \log K = & 30.9 \end{array}$$

By inserting the value for sea water:

$$\log[HAsO_2] - \log[HAsO_4^{--}] = 30.9 - (4 \times 8.1) - (2 \times 12.5) = -26.5$$

Thus, $HAsO_4^{2-}$ would be the predominating form at equilibrium.

Selenium. From the equilibria

$$\begin{array}{ll} SeO_4^{--} + H_2O + 2e^- \rightleftharpoons SeO_3^{--} + 2OH^-, & \log K = 1.7 \\ 2H^+ + 2OH^- \rightleftharpoons 2H_2O, & \log K = 28.0 \\ SeO_4^{--} + 2H^+ + 2e^- \rightleftharpoons SeO_3^{--} + H_2O, & \log K = 29.7 \end{array}$$

By inserting pH = 8.1 and pE = 12.5, we find $[SeO_3^{--}]/[SeO_4^{--}] = 10^{-11.5}$, which would indicate that SeO_4^{--} predominates at equilibrium.

Some Possible Solubility Equilibria

Strontium and Barium. The logarithms for the zero activity solubility products have been given as follows: $SrSO_4$ −6.6 (5°C, 25°C); $SrCO_3$ −10.0 (25°C); $BaSO_4$ −10.2 (5°C), −10.0 (25°C); $BaCO_3$ −9.3 (25°C). The difference $\log\,[SO_4^{--}]$ − log

$[CO_3^{--}]$ would then be about -0.7 at equilibrium with $BaSO_4$ + $BaCO_3$; and about 3.4 at equilibrium with $SrSO_4$ + $SrCO_3$. In sea water, the value for this difference is approximately $3.71 - 1.55 = 2.2$ at 5°C, and $3.49 - 1.55 = 1.9$ at 25°C. So it seems that in sea water, $BaSO_4$ and $SrCO_3$ might be stable solid phases, but not $BaCO_3$ or $SrSO_4$.

For equilibrium with $BaSO_4$ we calculate $\log [Ba^{++}] = -10.2 + (2 \times 0.8) + 1.55 = -7.0$, whereas the analytical values range between -6.2 and -7.4.

At equilibrium with $SrCO_3$ we would find $\log [Sr^{++}] = -10.0 + (2 \times 0.8) + 3.7 = -4.7$, whereas the analytical value for sea water is around -3.8. The actual concentration of Sr^{++} is thus, as for Ba^{++}, higher than the calculated one. One reason may be that we have underestimated the correction for activity factor, $-\log f_2$; for $SrCO_3$, Townley *et al.* (1937) give activity coefficients in NaCl solution that would correspond to $\log f_2 \approx -1.3$ in sea water, and give a practically perfect agreement with the observations.

In conclusion, it seems likely that $SrCO_3$ and $BaSO_4$ would exist as solid phases at equilibrium. Since these elements are present in small amounts, it may be that a considerable part of Sr and Ba is present in solid solution in, for instance, the silicate or $CaCO_3$ phases.

Cobalt. We may start with the equilibria

$$CoO_2\ (s) + H_2O + e^- \rightleftharpoons CoOOH\ (s) + OH^-, \quad \log K = 10$$

$$CoOOH\ (s) + H_2O + e^- \rightleftharpoons Co(OH)_2\ (s) + OH^-, \quad \log K = 2.9$$

In sea water, $\log \{OH^-\} - \log \{e^-\} = 8.1 - 14.0 + 12.5 = 6.6$, which shows that the first reaction goes to the right and the second to the left. Thus, of the stable phases mentioned, only CoOOH would be stable. Combining the second formula with

$$Co(OH)_2\ (s) + 2H^+ \rightleftharpoons Co^{++} + 2H_2O, \quad \log K = 12.4$$

$$H^+ + OH^- \rightleftharpoons H_2O, \quad \log K = 14.0$$

gives

$$CoOOH\ (s) + 3H^+ + e^- \rightleftharpoons Co^{++} + 2H_2O, \quad \log K = 29.3$$

At the conditions of sea water, then, $\log [Co^{++}] = 29.3 - 3\text{ pH} - \text{pE} - \log f_2 = 29.3 - 24.3 - 12.5 + 0.8 = -6.7$. The analytical values for the total Co concentration in sea water are from $10^{-7.9}$

to $10^{-8.8}$, which is of the expected order of magnitude; the cause of the little difference may be that CoOOH is present as a solid solution, perhaps with FeOOH

Nickel. The equilibrium

$$NiO_2\ (s) + 2H_2O + 2e^- \rightleftharpoons Ni(OH)_2\ (s) + 2OH^-, \quad \log K = 16.6$$

would indicate that $Ni(OH)_2$ (s) is stable, but not NiO_2, at the pH and pE of sea water. On the other hand, the equilibrium

$$Ni(OH)_2\ (s) + 2H^+ \rightleftharpoons Ni^{++} + 2H_2O, \quad \log K = 10.8$$

would give $\log [Ni^{++}] = 10.8 + 0.8 - (2 \times 8.1) = -4.6$, whereas the analyses of sea water are from -7.0 to -8.9. So, neither $Ni(OH)_2$ seems to exist at equilibrium as solid phase. With $NiCO_3$ as solid, (solubility product given as 10^{-8}), much too high Ni concentrations will also be calculated. It is possible that the concentration of Ni^{++} is determined by equilibria solid solution/aqueous solution.

Copper. From Näsänen and Tamminen (1949) we may take (25°C, zero activities):

$$CuO\ (s) + H_2O \rightleftharpoons Cu^{++} + 2OH^-, \quad \log K = -19.66$$

$$Cu(OH)_{1.5}(SO_4)_{0.25}\ (s) \rightleftharpoons Cu^{++} + 1.5OH^- + 0.25SO_4^{--}, \quad \log K = -17.12$$

$$Cu(OH)_{1.5}Cl_{0.5}\ (s) \rightleftharpoons Cu^{++} + 1.5OH^- + 0.5Cl^-, \quad \log K = -17.27$$

For equilibrium between the hydroxide-chloride and hydroxide-sulfate, we would have

$$0.5 \log \{Cl^-\} - 0.25 \log \{SO_4^{--}\} = -17.27 + 17.12 = -0.15$$

By inserting the values $\log \{Cl^-\} = -0.26 - 0.2 = -0.46$, and $\log \{SO_4\} = -1.55 - 0.8 = -2.35$, we find the difference $-0.23 + 0.59 = 0.36$. This would mean that the hydroxide-chloride is somewhat more stable than the hydroxide-sulfate, but the difference is so small that it might be changed by the temperature variation of equilibria.

For equilibrium between CuO (s) and $Cu(OH)_{1.5}Cl_{0.5}$ (s), we find $0.5 \log \{OH^-\} - 0.5 \{Cl^-\} = -19.66 + 17.27 = -2.39$, whereas the difference in sea water is $0.5\ (8.1 - 14.0 + 0.46) \approx -2.72$. Here, too, we would have a small advantage for the hydroxide-chloride which may be reversed, however, if CuO enters some solid solution, like the "manganite." With the equilibrium constant at 25°C, we would estimate $\log [Cu^{++}] = -17.27 + (1.5 \times 5.9) + (0.5 \times 0.46) + 0.8 \approx -7.4$. An approximately equal amount would be present as $CuOH^+$, and would make the estimated $\log [Cu]_{total} \approx -7.1$. The analytical values are between -5.8 and -8.4, which is still of the correct order of magnitude. Some other copper complex may be present, such as $Cu(OH)_2$, but the chlorocuprate(I) like $CuCl_2^-$ would not seem to be significant at equilibrium.

Lead. At 25°C we have

$$PbO_2\ (s) + 4H^+ + SO_4^{--} + 2e^- \rightleftharpoons PbSO_4\ (s) + 2H_2O, \quad \log K = 57.0$$

Now, in sea water, the expression

$$-(4 \log \{H^+\} + \log \{SO_4^{--}\} + 2 \log \{e^-\})$$
$$= (4 \times 8.1) + 1.5 + 0.8 + (2 \times 12.4) = 59.7$$

Thus, PbO_2 seems to be stable but not $PbSO_4$. The formation of PbO_2 may be further favored if it forms solid solutions with some other phase, such as MnO_2.

From the equilibrium

$$PbO_2\ (s) + 4H^+ + 2e^- \rightleftharpoons Pb^{++} + 2H_2O, \quad \log K = 49.2$$

we find

$$\log [Pb^{++}] = 49.2 + 0.8 - (4 \times 8.1) - (2 \times 12.5) = -7.4$$

According to Olin (1960), for

$$Pb^{++} + H_2O \rightleftharpoons PbOH^+ + H^+, \log K = -7.9 \quad (25°C, 3M\ NaClO_4)$$

We may then estimate that in sea water of pH = 8.1, roughly equal concentrations of Pb^{++} and $PbOH^+$ are present. Moreover, $[PbCl^+]$ may be two to six times $[Pb^{2+}]$, so that altogether $[Pb]_{total}$ would be $10^{-6.8}$ to $10^{-6.6}M$. On the other hand, PbO_2 at equilibrium may be present not as the pure substance but in solid solution with, say, MnO_2. Since Mn is $10^{2.3}$ times more abundant than Pb, the activity PbO_2 (s) may then easily be only 10^{-1} to 10^{-2}, and the $[Pb^{2+}]$, etc., and $[Pb]_{total}$ calculated should be multiplied by this factor. The total concentrations reported in sea water, from $10^{-8.0}$ to $10^{-7.6}M$ are of the right order of magnitude.

Gold. The occurrence of gold in sea water has often attracted interest. It has been suggested that gold is mainly present as suspended particles of metallic Au. The total concentrations given are usually of the order of 10^{-10} to $10^{-10.7}M$, but values as high as 10^{-8} have been reported.

It may be of interest to study what the concentration of dissolved gold species would be at equilibrium with metallic gold. From the work of Bjerrum (Bjerrum and Kirschner, 1918; Bjerrum, 1948) we may take the following equilibrium constants (20°C, zero activities):

$$AuCl_2^- + e^- \rightleftharpoons Au\ (s) + 2Cl^-, \quad \log K = 19.2$$

$$AuCl_4^- + 3e^- \rightleftharpoons Au\ (s) + 4Cl^-, \quad \log K = 51.3$$

$$Au(OH)_4^- + 4H^+ + 4Cl \rightleftharpoons AuCl_4^- + 4H_2O, \quad \log K = 29.64$$

By inserting the values for sea water: $pE = 12.5$, $pH = 8.1$, $\log [Cl^-] = -0.26$, and neglecting the activities, we would estimate $\log [AuCl_2^-] = -7.2$, $\log [AuCl_4^-] = -14.8$, $\log [Au(OH)_4^-] = -11.0$. In addition, there would be some intermediate complexes like $Au(OH)_3Cl^-$. Obviously, $AuCl_2^-$ would predominate at equilibrium. Since its concentration would be considerably greater than the total concentration of gold usually found in sea water, we may conclude that metallic gold would probably not be stable in the long run in contact with sea water, and that the dissolved gold would be present chiefly in the form of $AuCl_2^-$.

Conclusion

During these calculations, it has struck me that the resemblance between our equilibrium model and the real system is often better than one might have hoped for at the onset. Perhaps calculations like these may tell something about which solid phases and which species in solution one may expect in the ocean. Especially I should like to point out the refinements that will be possible when enough is known to take the formation of solid solutions into account. The calculations have also stressed a number of gaps in our present knowledge on equilibria in solutions, for instance on phosphate complexes and on uncharged hydroxo complexes.

It is inevitable that much of what has been said here about the equilibrium model and the real system will be subject to revision as more data become available. If the tables with tentative formulas for species and solids can induce someone to make experiments to fill the gaps or to prove me wrong, then I feel that this paper has fulfilled some useful purpose.

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Chemistry in the Oceans

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STUDIES in marine chemistry have gone through several phases since its birth with the first quantitative assays of sea water by Torbern Bergman, the famed Swedish scientist, and Antoine Lavoisier, the father of modern chemistry, at the turn of the eighteenth century. The seas were depicted as arising from the washings of the surface of the earth by natural waters, and investigations on both its chemistry and that of the organisms had a significant role in the development of chemistry. As you are well aware, the elements bromine and iodine were discovered in sea salt and marine algal ash, respectively.

When the rather dramatic effects of primary plant production on the distribution of some chemical species in the oceans were established during the first several decades of the twentieth century, impetus was given to work on the fertility of surface waters and the results of the combustion of the organic material in the deeper waters.

In the mid-twentieth century some attention again has been focused on the inorganic chemistries in the oceans, work paralleling and reflecting advances made in the mother science, chemistry. The geochemical behavior of elements during their residence in the sea, subsequent to their introduction from the continents and atmosphere, has provided the background for many recent investigations.

Although the discovery of new elements is apparently limited to a small group of people working in the foothills of Berkeley, California, two naturally produced radioisotopes have been initially found in the marine domain. Both of these isotopes, Be^{10} and Si^{32} are produced in the upper atmosphere by the cosmic ray fragmentation of the earth's enveloping gases, Be^{10} from nitrogen and Si^{32} from argon. The beryllium isotope with a half-life of 2.7 million years was simultaneously found by groups led by Dr. James Arnold (1956) of Princeton and Dr. B. Peters (Goel *et al.*, 1957) of Bombay in the deep-sea sediments of the Pacific Ocean. Dr. Lal of Bombay and I (1959) have sought and observed Si^{32} in siliceous sponges taken from waters of the mixed layers.

In both cases the marine realm provides the unique sites for the accumulation of these radioactive species in amounts that are readily extractable for quantitative assay. These cosmic ray-produced isotopes come down to the land and sea surfaces in atmospheric precipitation but are heavily diluted in the relatively large amounts of stable silicon and beryllium contained in the continental surfaces, whereas in the oceans, the quantities of stable beryllium and silicon, at least in surface waters, are small and allow the specific activity, the disintegrations of the isotope per weight of its stable form per unit time, to attain reasonably high values.

The beryllium concentration in sea water (Merrill *et al.*, 1960) is of the order of 6×10^{-4} of a part per billion by weight. Hence, a 4000-m water column, representing the average oceanic depth, contains per square centimeter about the same amount of beryllium as a millimeter depth of average earth's crust which has for all practical purposes a uniform beryllium content of a few parts per million. Thus, two effects tend to reduce continental specific activities of Be^{10} to values lower than those of the marine environment: (*a*) mixing of the radioisotope with stable beryllium to levels on land greater than a millimeter; and (*b*) the runoff into the oceans of any of the isotopes taken up by the rivers. Hence, the authigenic minerals on the sea floor, solid phases that derive their components from the chemical species in sea water, readily revealed measurable quantities of Be^{10}.

Similarly, the low concentrations of silicon in surface sea waters, resulting from the assimilation of monomeric silicic acid and/or its ions by the photosynthesizing diatoms, suggest a promising medium for the attainment of high specific activities of Si^{32}. If we assume the depth of the mixed layer to be 100 m and to contain 15 micromoles of silicon per liter, a 1-cm^2 column of such waters contains about the same amount of inert silicon as 0.01 cm of earth's surface. We have found that a disintegration rate of one per minute, readily measurable, necessitates the extraction of roughly 100 g of opal or silicon dioxide. Such quantities are available from siliceous sponges living in environments of the mixed layer waters. For every 100 g of sponge-produced opal, the equivalent of 100 tons of sea water must have had its silicon depleted to zero by the activity of these animals. Deep-sea sponges require the equivalent of 10 tons of sea water to obtain a corresponding amount of silicon inasmuch as these waters contain on the average 10 times more silicon.

Let us now turn to the more general problem of chemical processes in the oceans. Chemical reactions take place at phase discontinuities, i.e., the atmosphere-hydrosphere, biosphere-hydrosphere, and sediment-hydrosphere interfaces. We shall focus our attention mainly on the reactions of sea water with the solid components of the sea floor.

We can reasonably expect that most inorganic species correspond closely to those predicted from complete equilibration between all reacting substances. Such thermodynamically unstable species as iodide and manganous ions probably exist because the waters that contain them have been inaccessible to surfaces at which reactions to stable substances might occur. We shall return to this concept in considerations of the formation of ferromanganese minerals on the sea floor.

Insight into the *relative reactivities* of elements in the marine hydrosphere has been obtained from considerations of the average time an element spends in the oceans. An extremely simple model of the ocean is used in which it is assumed that the presently observed chemical composition represents a steady state system in which the amount of material introduced per unit time is compensated by an equal amount deposited as sediments. A further assumption is that there is a complete mixing of materials introduced into the oceans in times that are short with respect to the residence times. We can then define the residence time of an element as the total amount of the element in sea water divided by the amount of the given element introduced by the rivers or precipitated to the sediments per unit time.

About seven years ago Barth (1952), on the basis of river influxes of the elements, initiated such calculations, and his data are shown in Table I. An alternate approach has been made upon the basis of the total amount of sedimentation in the marine environment (Goldberg and Arrhenius, 1958), and the residence times so derived also are shown in Table I. A remarkable agreement is observed between these sets of data. The only striking discrepancy is found for the case of calcium. The many difficulties in trying to obtain a geochemical balance for this element are well known, and we certainly have not been able to resolve this difficulty, at least within a factor of 8.

Although many independent assumptions are involved in the calculations, both the absolute and relative values for most of the residence times appear reasonable. Sodium has a residence time within an order of magnitude of the age of the oceans, several billion years. This lack of reactivity is in accord with its aqueous chemistry. The alkali and alkaline earth metals have residence times in the range of 10^6 to 10^8 years. Manganese shows a remarkably low value, 7000 years, especially in comparison with the metals nickel and zinc, which probably have similar chemistries

TABLE I. Residence Times of Elements in the Oceans

Element	Amount in Oceans, g	Residence Time, Years	
		Goldberg and Arrhenius (1958)	Barth (1952)
Na	1.47×10^{22}	2.6×10^{8}	2.1×10^{8}
Mg	1.8×10^{21}	4.5×10^{7}	2.2×10^{7}
Li	2.8×10^{17}	2.2×10^{7}	
Sr	9.8×10^{18}	1.6×10^{7}	
K	5.3×10^{20}	1.1×10^{7}	1.0×10^{7}
Ca	5.6×10^{20}	8.0×10^{6}	1.0×10^{6}
U	5.2×10^{15}	6.5×10^{5}	
Zn	1.4×10^{16}	1.8×10^{5}	
Cu	5.2×10^{15}	6.5×10^{4}	
Co	7.0×10^{14}	1.8×10^{4}	
Si	5.2×10^{18}	1.0×10^{4}	3.5×10^{4}
Pb	$<4.0 \times 10^{11}$	$<1.0 \times 10^{4}$	
Mn	1.4×10^{15}	7.0×10^{3}	
Th	$<2.8 \times 10^{13}$	$<1.4 \times 10^{3}$	
Fe	1.4×10^{16}	1.4×10^{2}	
Ti	1.4×10^{15}	1.6×10^{2}	
Al	1.4×10^{16}	1.0×10^{2}	

in the divalent state and are associated with manganese in marine deposits. The residence times of these latter elements are about 500 times higher. This reactivity of manganese is apparently related to the removal of this element from solution by oxidation to the tetravalent state to form the ferromanganese deposits, a subject we shall discuss subsequently. The sorption of the associated metals like zinc and nickel to the precipitated manganese requires a relatively larger amount of manganese. This results in longer residence times, compared to manganese, for these metals.

Silicon and aluminum are among the elements with the shortest calculated residence times. Both elements enter the oceans in both solid and dissolved phases; the solid phases, such as quartz, feldspars, and clay minerals, rapidly settle to the bottom. Iron and titanium which also quickly pass through the hydrosphere, prevail as solid phases during the major part of their residence. The absolute values for the residence times of these elements are somewhat tenuous as the assumption that such times are small in comparison with the mixing times of oceanic water masses, say of the order of hundreds to thousands of years, is invalid. It may be worthwhile in the future, when values exist for the contribution of solid and dissolved phases of these elements to the total concentrations, to calculate more accurately the residence times of the components.

The utility of such computations, the derivation of residence times, arose recently in our laboratory in the study of thorium isotopes as a dating tool for marine sediments. We were concerned primarily with two isotopes, normally occurring thorium, Th^{232}, and ionium, Th^{230}, which is one of the daughter products of the most abundant isotope of uranium, U^{238}. The residence of thorium can only be given in terms of an upper limit inasmuch as the thorium concentration in sea water has never been determined. A value of a life in sea water of less than one thousand years, probably closer to one hundred years, is derived for thorium on the basis of a maximum concentration in sea water of 10^{-8} g/liter.

The extremely short residence time of thorium suggests the possibility of ocean to ocean variations in its concentration. Those bodies of water exposed to the introduction of large amounts of continental runoff may very well be enriched in normally occurring thorium compared to sea waters which are isolated from land drainage for times comparable to the residence time of thorium.

The uranium-derived isotope of thorium, Th^{230}, provides a convenient normalization for intraocean comparisons of thorium contents. Uranium has a residence time of the order of a million years, a time that is long with respect to oceanic mixing processes. Hence, one would expect and one does find a uniform content of uranium in sea water, a value around 3.5 μg/liter. Thus, the rate of production of its daughter ionium per unit volume of sea water is constant in all oceans. The ionium input from land is less than one-fourth of this oceanic production value and is unimportant in our considerations. Since the aqueous chemistry of thorium involves only one valence state, we can make the initial assumption that both thorium and ionium will be present in the oceans in similar chemical forms. Thus, we shall seek out the ratio of ionium to thorium as a measure of possible thorium variations in the ocean.

Although the thorium content of sea water is so low that its actual value so far has escaped detection by modern analytical techniques, some surface minerals on the sea floor, which accumulate thorium in measurable amounts from the over-lying sea waters, should provide a convenient index of the sea water concentrations. The thorium isotopic ratios given in Table II were obtained from the authigenic minerals in the upper 2 or upper 4 cm of deep-sea sediments. The lowest values of thorium compared to ionium are found in the South Pacific Ocean whereas the highest numbers occur in the Atlantic Ocean. Intermediate values are found in the North Pacific.

These values are reasonable when one looks at the relative

TABLE II. Values of Ionium/Thorium Ratio in Hydrogenous Minerals from Surface Sediment Samples

Area	Io/Th, Units of Disintegrations of Ionium/Disintegration of Thorium/Unit Time
Atlantic	12
North Pacific	25
South Pacific	150

contribution of land runoff waters to these oceanic areas. Table III gives the areas of the oceans and the respective areas of land that are drained into the oceans. The Pacific receives but one-sixth of the amount of drainage waters that enter the Atlantic on an areal basis, which apparently accounts for the higher values of thorium, normalized to ionium, in the Pacific sediments. Similarly, the well-known observation that more and larger rivers drain into northern hemispheric marine areas is reflected in the higher ionium/thorium ratios in southern Pacific deposits as compared to their northern counterparts. Thus, the concentration of thorium in the deeper parts of the ocean is seen to have an ocean to ocean variation, explainable, on the basis of our simple thesis of the residence time of thorium being small with respect to the times of oceanic mixing, coupled with the yearly contributions of thorium draining into the world's oceans.

Let us now turn to a rather dramatic example of chemistry occurring on the sea floor, the formation of the ferromanganese minerals, the major components of the manganese nodules. These minerals represent the most nearly unique and possibly the most abundant, and for these reasons, the most studied of the marine authigenic minerals. They exist in the form of nodular concretions which range in size from millimeters to about a meter, coatings about rocks and shells, and as components of the unconsolidated sediments. The two principal metals, iron and manganese, which occur as oxides or hydroxides, are normally present in similar amounts, although, less generally, either of these two elements can be dominant. They are found on all oceanic floors and normally occur in localities where the total rate of accumulation of sediments

TABLE III. Oceanic Areas and Complimentary Land Areas Draining into Them (in thousands of square kilometers) (Lyman, 1958)

Ocean	Area	Land Area Drained	Percentage
Atlantic	98,000	67,000	68.5
Indian	65,500	17,000	26.0
Antarctic	32,000	14,000	44.0
Pacific	165,000	18,000	11.0

is low. Menard and Shipek (1958) estimate that between 20% and 50% of the deep-sea floor in the southwestern Pacific is covered with nodules on the basis of the photographs of the bottom and the occurrence of nodules in cores. Phillipsite, barite, and fish debris, phases which are strongly diluted in rapidly amassing deposits, are found in high concentrations in areas associated with ferromanganese minerals.

The ferromanganese minerals act as hosts for a suite of elements which include copper, nickel, cobalt, zinc, lead, thorium, and the rare earths. These guest metals, which are enriched in the ferromanganese minerals, as well as the manganese, exist in sea water in states of undersaturation (Goldberg, 1958), and their assimilation by these minerals has been postulated to account at least in part for this situation.

Their unique chemical composition, unlike that of any terrestrial mineral has strongly indicated the authigenic character of the ferromanganese accumulations (Table IV). Further support comes from the lead isotopic analyses of Chow and Patterson (1959), who point out that the distinctive values of the radiogenic lead isotopes suggest a derivation of the lead from sea water.

TABLE IV. Average Composition of Manganese Nodules from the Pacific Ocean

Element	Weight %
Fe	14
Mn	19
Ni	0.4
Co	0.3
Cu	0.5
Ti	0.8
Zn	0.04
Pb	0.1
P	0.5
Al	0.7
Zr	0.006

Structural investigations by Buser and Grütter (1956) by x-ray and electron microscopic techniques indicate the minerals are composed of the crystalline iron and manganese compounds, δ-MnO_2, manganites and goethite, as well as some amorphous fractions. δ-MnO_2 is composed of disordered sheets of manganese dioxide, whereas the manganite crystals possess a double layer-lattice structure in which ordered layers of manganese dioxide alternate with disordered layers of manganous or ferric hydroxides or basic salts. The disordered layer is the site for the accumulation of the metal ions whose enrichment in these materials has been pointed out previously. In nodules with amounts of iron, greater than can be accommodated in the disordered layer, the mineral goethite appears. Buser (personal communication) points out that the appearance of goethite in the minerals suggests that particles of fresh iron hydroxide, or oxides of lower molecular weight, are initially deposited, which possess the potentiality of transformation to goethite.

The rates of accretion of these minerals on surfaces or during formation of the nodules is extremely slow. The "Horizon" nodule, a large concretion dredged from the North Pacific with a longest dimension of about 1 m, was analyzed by the ionium-thorium method and was found to amass its solid phases at a rate of somewhat less than 0.01 mm per thousand years or a rate of about one atomic layer per day. This is probably one of the slowest reactions occurring in nature in which a measure of the rate of the reaction can be ascertained. It should be emphasized that such rates are not necessarily continuous, as often layers of clay or detrital materials are found between the slowly accreting ferromanganese lamina.

The rather exotic nature of these minerals has inspired a number of hypotheses as to their mode of formation. The early workers were more concerned with the immediate origin of the manganese and associated elements, rather than any physicochemical considerations. Such sources of manganese as Foraminifera, volcanic debris, and subsurface springs were postulated. Further, both biochemical and inorganic mechanisms to deposit the manganese and iron oxides were invoked. Of special interest today is the thesis of biological oxidation, first proposed by Dieulafait (1883), taken up again by Dorff (1935), and recently revived by Graham (1959). I shall return to this problem somewhat later.

A satisfactory hypothesis must account not only for the chemical and physical characteristics of the materials, but also for the geological observations concerning their occurrences. Thus, whereas manganese is in a reduced, dissolved state in sea water, in the ferromanganese minerals it is in both the divalent and tetravalent forms, although mainly the latter. The only nonbiological species in the ocean in sufficient amounts capable of oxidizing manganese is dissolved gaseous oxygen and the reaction

$$2OH^- + Mn^{++} + \tfrac{1}{2}O_2 = MnO_2 + H_2O$$

has a free energy of -9 kcal at a pH of 8, a manganous ion concentration of $10^{-9}M$, and a partial pressure of oxygen of 0.25 atmosphere. All these concentrations are similar to those in near-bottom sea waters.

Since tetravalent manganese is not found in sea water, although from the above data it is the thermodynamically stable form, a reaction site or surface is probably necessary for the reaction to proceed. The well-known catalytic properties of iron oxide surfaces suggest the association of such material in the formation of the nodules. Iron exists in sea water dominantly in particulate phases, partly collodial. The accumulation of iron oxides on surfaces, where either the bottom topography or the lack of sediment source material does not allow any appreciable accumulation of solid phases, would initiate formation of the ferromanganese minerals. In areas of rapid deposition, where nodules or accretions are not found, the burial of any iron oxide surface by other sediment components minimizes any mineral formation.

The catalytic oxidation of manganese on the oxide surfaces leads directly to the formation of the ferromanganese minerals. Where an excess of iron is accommodated, the mineral goethite appears. The scavenging of the reactive, high charge density ions from sea water, those previously described as having relatively short residence times, and their incorporation into the disordered layer follow. The formation of the new mineral surface, allowing sites for further oxidation of manganese, i.e., the reaction becomes autocatalytic, completes the picture.

The recent and significant observation by Graham (1959) that these nodular materials contain appreciable amounts of organic matter has resulted in the revival of the hypothesis of biological origin. Although bacteria and other organisms have been sought on the nodules by previous investigators, possibly with not enough elegance, and not found, the enthusiasm of the adherents of biochemical theories has not been dampened.

The alternate hypothesis that the organic matter in the nodules was adsorbed from sea water appears plausible. The ferromanganese minerals possess rather high specific surface areas, ranging from 6 to 190 m^2/g (Buser and Grütter, 1956), reactive sites capable of the uptake and retention of organic phases. Further, it is conceivable that bacterial activity does take place at such surfaces and that benthic organisms might not be attracted to such material. But an extension of such thought to a direct biological deposition at the present time seems unwarranted.

On a biochemical basis, it is very difficult to account for the relative proportions of certain metals in these minerals, two in particular, cobalt and cerium. Cobalt exists in sea water at a concentration of about one-seventh that of nickel (Taivo Laevestu, personal communication) on the basis of recent, refined analyses. Although cobalt and nickel show a strong geochemical coherence in behavior during the major sedimentary cycle, the ferromanganese phases contain nearly as much cobalt as nickel on the average (Table IV). Cobalt shows a wider spectrum of concentrations in nodules than does nickel.

An explanation for these abundances may well be found in the greater ease of oxidation of cobalt from the divalent to the trivalent state. The oxidation potential of cobalt for such a reaction is slightly higher than that for manganese and the free energy of the reaction, using typical marine concentrations, appears to be positive, i.e., the reaction should not proceed. However, a combination of the cobalt and manganese oxidation reactions to form a solid solution of the cobalt oxides in the manganese dioxides gives a thermodynamically possible reaction, which could result in a fractionation of cobalt over nickel. Where the redox potential of the environment is relatively low, the cobalt/nickel ratios of sea water would be expected in the nodules, as only the divalent ions are involved. Thus, the cobalt/nickel ratios may well be a sensitive indicator of the oxidation environment in the vicinity of ferromanganese mineral formation.

Cerium, one of the rare earths susceptible to oxidation to a higher state than the normal plus three, is enriched in these minerals relative to its periodic table neighbor lanthanum, which exists solely in the trivalent state. In ferromanganese minerals, in which cerium is apparently oxidized in part to the plus four valence state, the cerium/lanthanum ratio normally is of the order of six, although this value was over an order of magnitude higher in the case of a Triassic nodule from Timor. Whereas in crustal rocks on the earth's surface, the cerium/lanthanum ratio is about three. Hence, it is proposed that the oxidation of cerium, which like that of cobalt is not evident from thermodynamic considerations, proceeds through the incorporation of ceric oxides into the manganese dioxide lattice with a coupling of the manganous and cerous oxidation reactions. The high concentrations of metals susceptible to oxidation offer a dilemma to any biological hypotheses. Are we to have not only manganese oxidizing capabilities in the organisms but also cerium and cobalt oxidizing capacities?

I do not wish to leave a picture of chemical reactions on the sea floor not influenced by the large biomass of the oceans. The plants and animals of the seas are responsible for the most dramatic compositional changes in the oceans. In the surface waters where plant production occurs, carbon dioxide and oxygen, the intake and release gases of photosynthesis, respond to this biological activity. Depletion of the former and supersaturation of the latter are often observed in waters near the surface. Also, the plant nutrients, chemical species of phosphorus, nitrogen, and silicon vary over wide ranges of concentrations both in time and space.

Barium is one non-nutrient element which shows very positive correlations between concentrations in sediments and biological activity. Concentrations of this element are markedly higher in pelagic sediments below productive oceanic areas than in bottom samples below the more barren seas (Goldberg and Arrhenius, 1958; Goldberg, 1958). The high barium contents are associated with both siliceous and calcareous deposits, although the concentration of this element is not markedly high in the siliceous or calcareous hard parts of organisms. The barium is probably accumulated in the sediments through chemical reactions involving the organic debris.

A clue to the marine geochemical behavior of barium may be found in its distribution in sea water. Dr. T. Chow and I have recently found barium existing in sea water in a state of undersaturation with respect to precipitation of the sulfate and with concentrations ranging between 10 and 70 μg/liter. The lower values are found in surface waters, and there is a consistent increase in barium content with depth. The depth profiles are somewhat similar to those previously reported for radium.

Possibly, the release of high concentrations of sulfate ion, resulting from the oxidation of organically bound sulfur in biological debris in the oceans, can result in a consequential precipitation of barium sulfate in the microenvironment of this organic material. As simultaneous sinking and combustion of this organic matter occurs in the oceans, part of the incorporated barium may be returned to the sea water through dissolution of the barium sulfate. Part of the barium may end up in the sediments. Further, one can conceive that any oxidation of organic matter in the sediment may result in the uptake of barium by the mechanism illustrated above. Such processes would result in an increase in barium with depth and its accumulation on the sea floor.

Early German and Russian workers pointed out the striking accumulation of heavy metals over sea water by a whole spectrum of marine organisms. Iron, vanadium, zinc, and nickel were amassed by the biosphere to average enrichments over sea water by factors of tens of thousands. Recently, a wealth of values on the heavy metal contents of members of the marine biosphere has resulted from problems involving the disposal of radioactive wastes and bomb fallout. Such work has strengthened the observation of the concentration of heavy metals in organisms of the sea. These metals are retained by strong chemical bonds and cannot be eluted (washed out) by repeated rinsings with fresh or sea waters.

The relative concentration factors of metals in the marine biosphere as compared with those of sea water closely parallel the order of stability of metal ions with a variety of organic complexing agents (Goldberg, 1957). If one takes the stability constants of metals forming organic complexes with a large suite of organic complexing agents, independent of the functional group, the increasing order of stability for the metals shows a co-variance with the relative enrichment of the metals in marine organisms. The animals and plants of the sea provide a huge reaction area for the uptake of dissolved metallic ions. One governing factor for the uptake of specific ions in competition with other ions is the equilibrium constants of the chelating reactions.

Concepts in modern chemistry should provide an entry into the resolution of the host of problems confronting the marine chemist. Why, for example, do manganese nodules close to coastal areas contain extremely high amounts of manganese compared to iron? A nodule recently dredged from the Gulf of California contained essentially pure MnO_2 and was devoid of the normally associated metals such as nickel, cobalt, zinc, and copper.

What is the intimate chemistry involved in the formation of phosphorites and glauconites on the sea floor? What redox conditions are required for their buildup and what associations with the biochemistry of the seas, if any, are involved?

The distinction between detrital and authigenic clay minerals is not clear-cut, if it can ever be. It has been known since the early thirties, after the work of Goldschmidt, that boron is enriched in marine, compared to continental, clays. Marine sediments contain hundreds of parts per million of boron whereas continental clays contain but one-tenth to one-twentieth of this amount. The boron is strongly held in the clay lattice, not removed by various washing or chelating elements. Where does it sit in the clay lattice? Boron, much more abundant in the oceans than in terrestrial waters, may well enter the clay structure or additions to the already existing minerals resulting in higher contents of this element in marine clays. Any continental clays introduced into the oceans would obtain their boron on the sea floor rather than during their passage to the sea floor because of the much longer time periods. The problem of detrital versus authigenic marine clays in the extreme reverts to the classical conundrum of the sock which is repeatedly darned until none of the original material is left. Is this a new sock or not? A continental clay rearranges on the sea floor. Is this a new clay or not?

These are but a few of the problems that may be found in the chemistries at the sea floor-sea water interface. Solutions will be found not solely in the bases provided by modern chemistry, but only in the coupling of such knowledge with the physical, biochemical, and geological processes in the oceans.

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Vertical and Horizontal Movements in the Ocean

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SINCE Stommel (1958) published his book on the Gulf Stream, there is no need for another review of vertical and horizontal transport in the Atlantic. Instead I propose to describe an experimental investigation at one station, Cavall, in the Bay of Biscay at 46°30′N, 8°00′W.

For seven years we have there been studying vertical and horizontal movements. To do so we have had to study changes in depth, temperature, salinity, oxygen, and silicate which are little greater than the experimental errors of the methods used. We have been improving our own technique but only in 1959 were we satisfied that our results would support the interpretation we wished to put upon them. Before conclusions can be presented, some assessments of error need to be made. Except in Tables I and II *potential* temperature and *potential* density will be used. No measurements with current meters have been made.

Four-Thermometer Water Bottles

In our earlier records many cases occur where depth readings on adjacent bottles on a hoist were in poor agreement. We have uncertainties of as much as 40 m in some of our depths, and uncertainties of 20 m were commonplace. The thermometers were blamed. In consequence the Laboratoire Oceanographique, Copenhagen, made for us a number of water bottles to carry four thermometers, two protected and two unprotected. The various external fittings of the water bottle have to be repositioned to obtain a convenient four-thermometer design. At the New York Congress I learned that other laboratories have also recently employed similar instruments. Our idea was that we should be able to pick out evidently discordant temperatures from a set and to reject them. In 1958 the agreement between paired unprotected thermometers was much better than expected. Paired unprotected thermometers agreed well. Rogue readings were scarce. The discrepancies are no more than we should get by assuming that thermometric error in a depth measurement is no greater for unprotected than for protected thermometers and that the error in depth measurement is the statistical sum of error for the two types of thermometer and for the pressure coefficient.

We cannot account for the anomalies in depth in earlier years as due to malfunctioning of unprotected thermometers. The apparent discrepancies in depth measurement have proved to be due to "vertical yawing." Research ships may resemble R.R.S. *Discovery II* from which it is possible to maintain a nearly vertical wire angle even in a moderate gale or our own vessel *Sarsia* from which it is not.

Vertical Yawing

Our troubles seemed to be confined to occasions when *Sarsia* had to work in strong gusty winds. When our wire has been near vertical we have had no trouble. However, when the hydrographic wire enters the surface of the sea at a considerable angle (Fig. 1), the thrust of the water on the wire and the mass of the wire, the bottles and the sinker attached to the wire result in a curved wire. The bottom part of the wire will be much more nearly vertical than the top part. To simplify the argument, it will be assumed that the bottom part of the wire is indeed vertical.

A gust of stronger wind will cause the speed of drift to increase. At the surface, the wire angle will increase and at all depths at which the wire is curved there will be a force normal to the wire tending to prevent the wire straightening out. From this force a vertical component may be resolved which tends to lift the wire, and everything carried by it, through the water. The depth of the hoist of bottles will become less. Now let the gust die away. The only force acting on the bottles will be that of gravity, tending to restore the wire to the vertical. The hoist of bottles will then

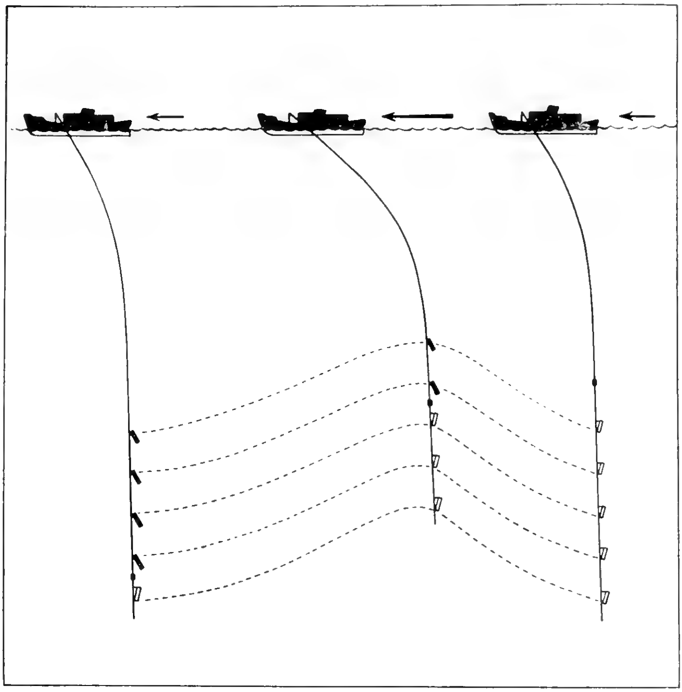

Fig. 1. To illustrate vertical yawing of a hoist of water bottles worked during windy weather from a ship which cannot maintain a vertical wire. The arrows represent direction and strength of a variable wind. (*Middle*) effect of a strong gust on the depth of the hoist of bottles; (*left*) what happens when the gust dies away. The messenger is shown running between bottles during the vertical yaw. On such a hoist thermometric depths may appear discordant as between water bottles while duplicate temperatures from the same frame may agree poorly.

sink. Consequently during gusty weather, there will be a tendency to vertical yawing of a hoist worked from a ship from which the wire cannot be maintained nearly vertical.

Table I presents data for a near vertical hoist. For such a hoist the difference between the duplicate temperatures is usually no more than 0.01°; a difference of 0.03° is exceptional. Similarly, a difference between paired measurements of depth as great as 11 m (as at 2200 m) is rather uncommon.

Table II presents data for a hoist with a surface wire angle of 45°. There are two differences in observed temperature of 0.03°

and one as large as 0.12° C. The paired determinations of depth at 1800 and 1900 m nominal are very concordant but the difference between them is 105 m, 5 greater than the distance between them (100 m) and 25 m greater than the depth intervals observed between the shallower bottles. There is no doubt that while the messenger was running between the bottom pair of bottles, the whole hoist sank by at least 5 m or, more likely, by 20 m.

Wüst (1932) studied the mean errors of thermometric measurements of depth during the *Meteor* expedition. At 1200 m he estimated the mean error as about ±7 m. In terms of precision, though not necessarily of accuracy, it is possible to improve on this by using paired unprotected and paired protected thermometers on each bottle.

In Table II if a uniform wire angle between 1400 and 1800 m nominal is considered to extend to 1900 m nominal, the depth of the bottom bottle would fall short by 18 m of that measured by paired thermometers. Since we have a number of other hoists with large wire angles which yield a similar answer, the interpretation of the results as due to vertical yawing seems reasonable.

Now that we have more accurate salinity measurements, the error introduced by vertical yawing is more serious than appears at first sight. There is not only error in depth but temperature and

TABLE I. Hoist of Average Quality Made with Small Wire Angle (10°) Station Bedivere, 20 April, 1958

Wire Depth, m	Observed Temperature, °C	ΔT, °C	Observed Thermometric Depth, m	ΔD, m	Depth Assuming Vertical Deep Wire, m	Error in Depth, m
1900	4.13 4.13	0.00	1875.8 1870.6	5.2	1871	−2
2000	4.06 4.05	0.01	1969.0	—	1971	+2
2100	3.73 3.72	0.01	—	—	2071	—
2200	3.66 3.67	0.01	2161.1 2172.0	10.9	2171	−4
2300	3.44 3.44	0.00	2273.8 2275.1	1.3	2271	+3

salinity also do not correspond. The flushing of our bottles is probably efficient so that the salinity represents the depth at which the bottle closed. Thermometers, however, require a few minutes to equilibrate. During gusty weather the thermometers can do no more than indicate some sort of mean value of the water through which the bottles are rising and falling. Moreover, each of a pair of thermometers is not likely to have the same rate of approach to equilibrium; nor are unprotected thermometers likely to respond at the same rate as protected thermometers. Consequently, during vertical yawing anomalous and discordant temperatures and thermometric depths are much more likely than when work is done with a vertical wire.

Since temperature and salinity may not quite correspond, a temperature-salinity plot will show excessive scatter about the best curve drawn through them. A measure of standard deviation will be larger than with samples drawn on a vertical wire.

At New York the very careful study of the yawing problem by Wüst (1932, pp. 140–149) was overlooked. Nevertheless no excuse is needed for raising the issue again. It will be essential not only to

TABLE II. Hoist with Large Wire Angle at Surface (45°) to Illustrate Vertical Yawing
Station Bedivere, 28 September, 1958

Wire Depth, m	Observed Temperature, °C	ΔT, °C	Observed Thermometric Depth, m	ΔD, m	Mean Observed Depth, m	Distance between Adjacent Bottles, m
0	—	—	—	—	—	14 × 73.6
1400	8.96	0.00	1029.2	3.9	1031	
	8.96		1033.1			78
1500	8.55	0.12	1103.0	11.0	1109	
	[8.67]		1114.0			
1600	7.87	0.03	—	—	—	2×90
	7.90					
1700	7.45	0.00	1289.8	3.2	1288	
	7.45		1286.6			79
1800	6.72	0.03	1367.0	0.2	1367	
	6.69		1367.2			105
1900	5.91	0.00	1472.2	0.1	1472	
	5.91		1472.3			

increase the precision of measurement by the new techniques and to establish with high precision the relations between the classical quantities and conductivity but also to ensure that new research ships should be able to maintain a vertical wire under all conditions when work is possible.

Salinity and Temperature-Salinity Diagrams

Our approach has been experimental. We have concentrated on five positions which, with the help of the Decca Navigator system, we are able to maintain within a circle of 1-mile radius. The main station Cavall in 4700 m of water is well out in the northern Bay of Biscay, 70 miles from the continental slope. This station is worked very intensively. Only the waters at Cavall below 1250 m will be discussed. The Gulf of Gibraltar water around 1000 m will be ignored.

Our salinities on deep samples from the cruises on R.V. *Sarsia* in March, April, and September, 1958, were determined by precision titration by Dr. Riley and Mr. Culkin at the University of Liverpool (Bather and Riley, 1953). The analyses in April were not so good as the rest, almost certainly due to changes during storage and transportation, and will not be used. The March and September figures were very consistent (Fig. 2). There is a change in both scales of four times at 5.5° and salinity 35.21‰. The slope is unchanged as between 5.05° and 8°, as had been established in earlier years. It is seen that the water between 5.05° and 8° is in neutral adiabatic equilibrium at a potential density 27.80 sigma-theta. There is no hindrance to complete mixing with the lower layers of the Gibraltar water, which I shall not discuss today. Although there are large changes in potential temperature and salinity, they completely and exactly compensate each other.

At depths greater than 1850 m, breakpoints were selected by inspection, linear curves being then fitted by the method of least squares. Around the curve covering depths between 1850 and 2600 m, the standard deviation was twice as great as for other ranges of depth, and indicated a source of variability other than experimental error. When the oxygen observations, to be discussed later, were taken into account, it became reasonable to construct

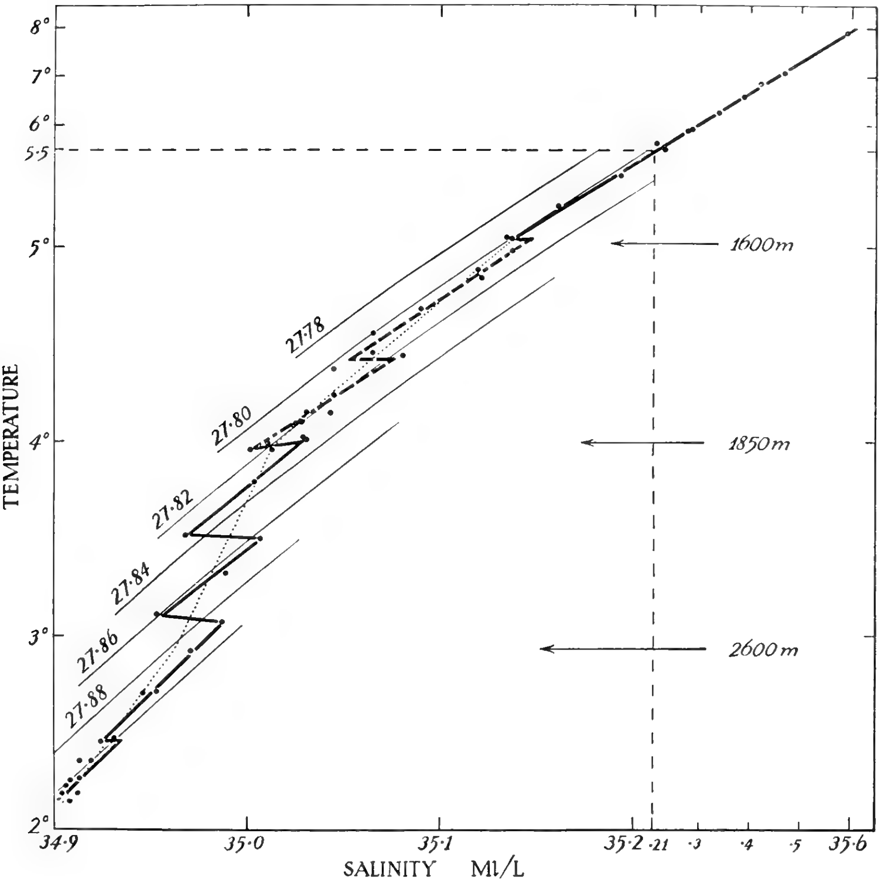

Fig. 2. A plot of salinity against potential temperature below 8°C at station Cavall (46° 30′N, 8°00′W) together with curves of equal potential density, March and September, 1958, combined but April omitted. The linear curves have been derived from the data by the method of least squares. The dotted lines between 1600 m and the bottom were drawn from the first breakdown of the T-S observations. The full lines below 1850 m were constructed subsequently in the light of the information given by the oxygen analyses and provide a better fit. The dashed lines between 1600 and 1850 m reconstructed similarly have a probability little greater than the original dotted line.

a steplike structure for the T-S observations between 1850 and 2600 m. In Fig. 2 the first approximation has been drawn as a dotted line and the later refinement in full line. We see that on this interpretation the observations are best fitted by a number of water masses each in neutral adiabatic equilibrium. Two further similar curves may be fitted between 1600 and 1850 m, but they follow from the thesis and are not evidence for it.

This paper was presented on 1 October, 1959, at Copenhagen at the meeting on the IGY preceding the International Council for the Exploration of the Sea. This sandwich-like structure was criticized during discussion on the grounds that if it existed it would have been recognized earlier. In reply one may say that it is only in very recent years that we have had the means by precision titration of chlorinity (Hermann, 1951; Bather and Riley, 1953) or by measurement of conductivity (Schleicher and Bradshaw, 1956) to obtain sufficiently refined data. Oxygen data also have had to be handled in a somewhat unusual way in order to yield the necessary precision.

There is no evidence at any depth of an apparent density inversion such as we and others had suspected on the basis of less precise Knudsen titrations.

It is of interest that extrapolation of the abyssal curve leads to the point: potential temperature, $-0.9°$; salinity 34.67‰; closely corresponding to the properties of the Antarctic bottom water in the Atlantic-Antarctic basin. This provides a simple means of estimating the amount of the Antarctic component in the eastern North Atlantic. Moreover, the nature of the curve suggests that water with an Antarctic component mixes upwards and in the Bay of Biscay vanishes sharply at 2800 m depth.

Relation between Potential Temperature and Oxygen

When our results were last reported part of our work had to be withdrawn at the last moment since we had established that in some of our samples there had been very considerable consumption of oxygen in the water bottles while they were being hauled in. We have now coated our bottles with an epoxy resin, Araldite, and seem to have completely eliminated this source of trouble.

First let us consider the water below 2500 m at station Cavall. Figure 3 epitomizes the four cruises in 1958. The standard deviation between duplicates does not exceed 0.04 ml/liter. Short-term variations of 0.1 ml/liter or so appear at all depths.

In November on board R.R.S. *Discovery II* it was convenient

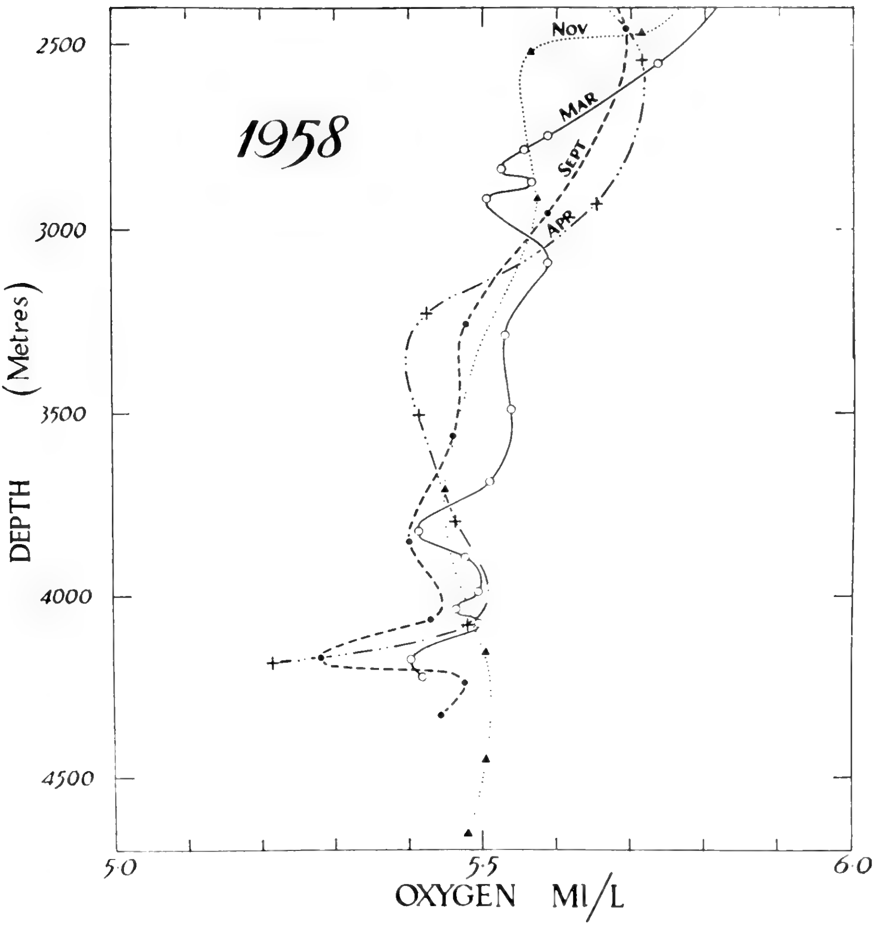

Fig. 3. The distribution of oxygen against depth at station Cavall on four occasions in 1958.

to work the station with a mixed hoist of bottles, some protected with Araldite, others not so protected. Four of the unprotected bottles were used within the range of depths covered by Fig. 4. Three of them came outside the envelope of our 1958 results obtained with Araldite-coated bottles, and have not been included within this discussion.

Many oceanographers are interested in long-term changes in the oxygen content of deep water. Standard practice in the past has

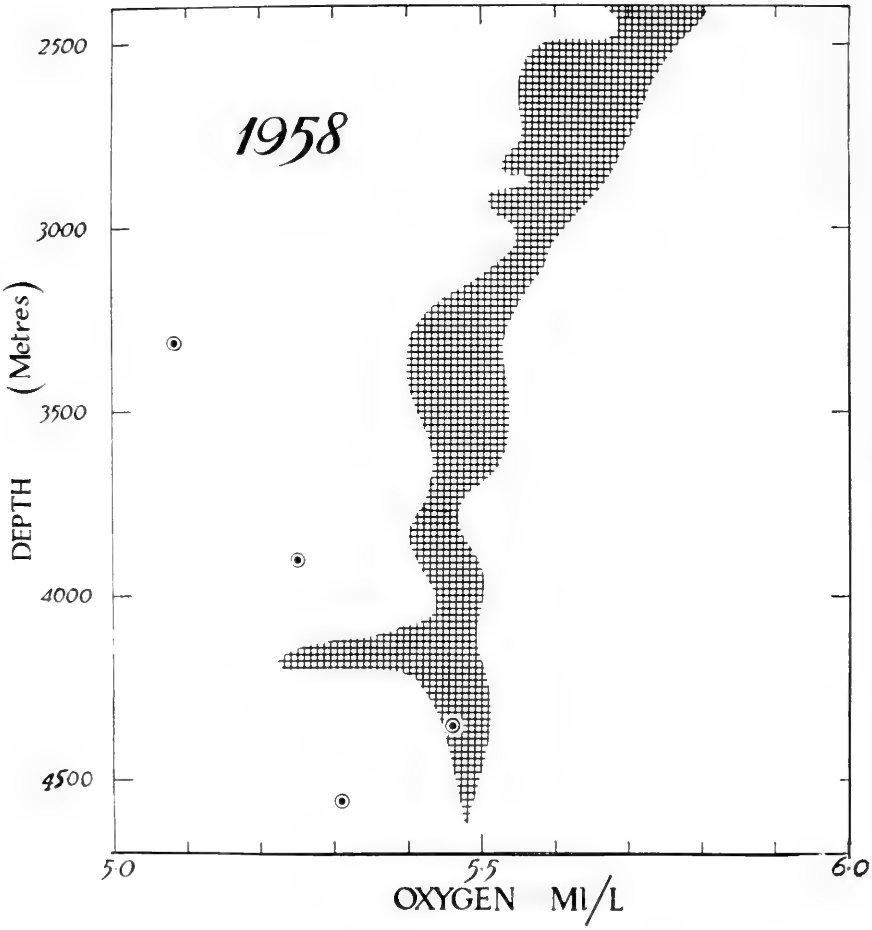

Fig. 4. Station Cavall, 1958. The crosshatched envelope includes all deep results on four cruises obtained from water bottles protected against corrosion by coating with Araldite. The four points are the mean of duplicates taken on the November cruise with water bottles not so protected.

been to work depths 500 m apart. In March we worked many more depths than this, and we worked them in duplicate (Fig. 5), in which are drawn two limiting curves each joining points 500 m apart. Consequently, with 500-m interval sampling we would have missed detail amounting to 0.1 ml/liter.

Figure 6 presents: (*a*) the envelope enclosing all our results in 1958; (*b*) the results of two cruises by the Danish Research

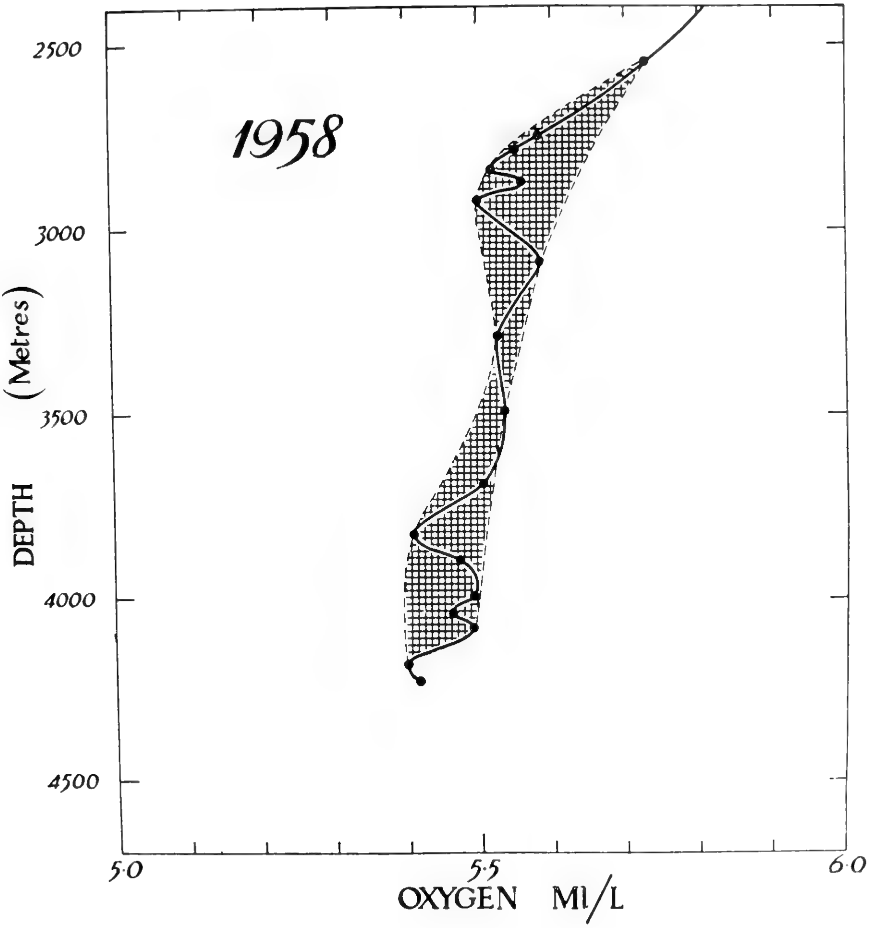

Fig. 5. Station Cavall, March, 1958. To illustrate the important detail in oxygen determinations which may be missed when deep stations are worked at 500-m depth intervals.

Vessel *Dana*, certainly with uncoated bottles and without unprotected thermometers for measuring depth; (*c*) the results of three cruises by R.R.S. *Discovery II*, using coated bottles and unprotected thermometers; (*d*) the results of two cruises by R.V. *Sarsia* in 1956 with water-bottles some of which are now known to have suffered from oxygen absorption by corrosion spots.

Even if the 1922 results of *Dana* suffered from oxygen absorption, they still are the highest ever. From 1922 through 1930 to

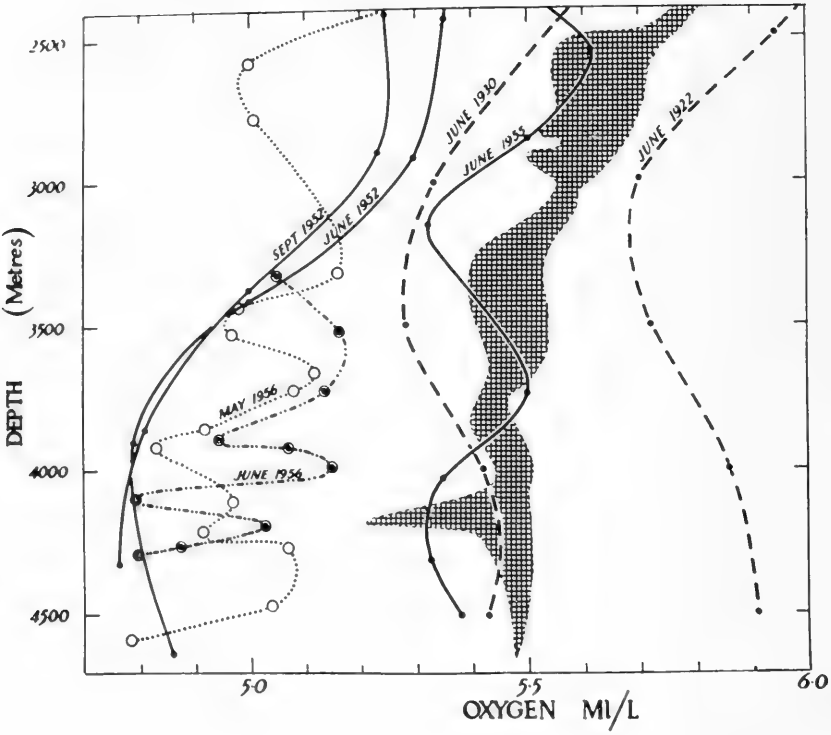

Fig. 6. Station Cavall below 2500 m; Change in oxygen content with time The crosshatched envelope includes all observations from four cruises in 1958 with Araldite-coated water bottles. The observations in 1922 and 1930, almost certainly from uncoated water bottles, may be too low. The observations from R.R.S. *Discovery II* in 1952 and 1955 were from coated water bottles. Those from R.V. *Sarsia* in 1956 were from uncoated water bottles and are all under suspicion.

1952 there was a drop in oxygen content of the abyssal water of nearly 1 ml/liter. Then in a further three years, half the lost oxygen came back. In 1955 conditions were not very different from those throughout 1958.

From the *Sarsia* observations in 1956 all the minima should probably be rejected but the maxima may be sound. If they are, there was a fall and a recovery of about 0.2 ml/liter between 1955 and 1958.

We see that there are large fluctuations at a single station within seven years which make it difficult to use this evidence to evaluate the age of the abyssal water in the eastern North Atlantic. A different approach is preferred—the evaluation of the fine structure of the deep water. At station Cavall in 1958, 340 separate analyses of oxygen were made. The data in March, April, and September are presented in Fig. 7, replicates being averaged. On the April cruise many very concordant analyses of oxygen were made but were not matched by salinities of equal value. Consequently April values appear on Fig. 7 but not on Fig. 2. The ranges of temperature have been adjusted from those first selected by inspection of the oxygen/potential temperature diagrams, but in doing so the standard deviations of observations

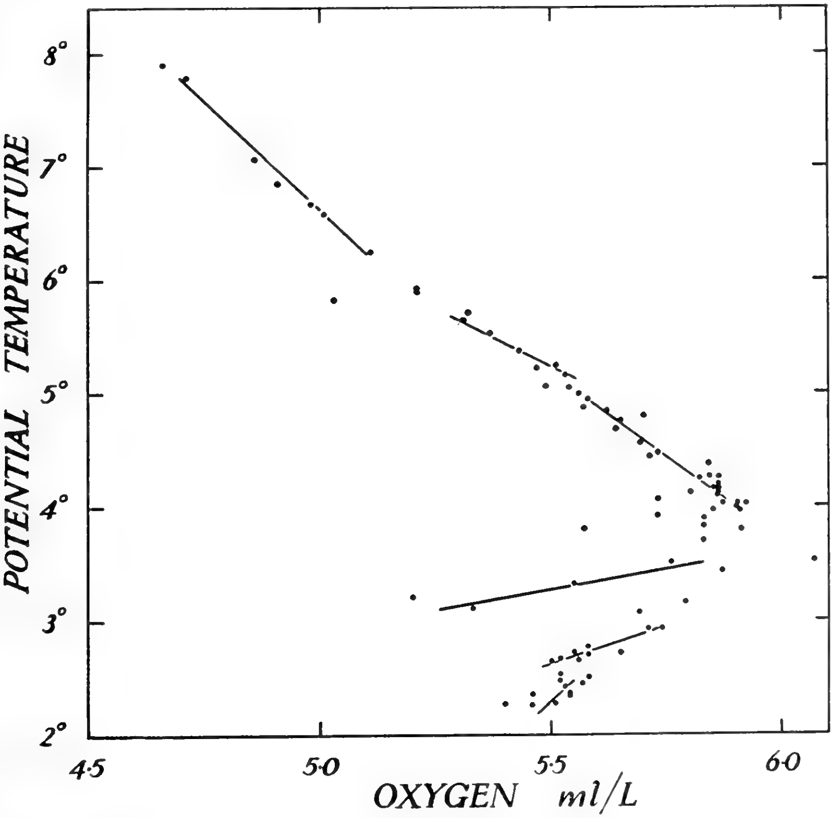

Fig. 7. Station Cavall, March, April, and September, 1958, combined. Curve fitting by method of least squares of oxygen/potential temperature observations.

from the curves of best fit have been reduced by as much as ten times.

Curves have been fitted by the method of least squares to both oxygen and salinity data to break down the deep water into a series of separate water masses. Although the two approaches are broadly concordant, they are no longer independent since each has been used to refine the inferences drawn from the other.

The water colder than theta 2.18°, lying in an enclosed basin, is in adiabatically neutral equilibrium, (sigma-theta = 27.903). The scatter of the oxygen analyses, confirmed by replication, is quite large but their discussion is better deferred.

The curves for both theta/S and theta/O_2 from about 2.18° to 2.40° (sigma-theta = 27.903) are reasonably coherent and show a layer in neutral equilibrium and simple mixing.

Around 2.50° curve fitting of the oxygen data is impossible while the salinity and temperature suggest a marked decrease in density. One has the impression of a zone of conflict between thin strata of contesting waters.

Between 2.64° and 2.92° (sigma-theta = 27.892) the observations are once more coherent and suggest another layer in adiabatic neutral equilibrium.

Around 3.0° there may be another zone of conflict, a large scatter in oxygen content and a sudden jump in density.

Between 3.2° and 3.5° observations are scanty but they are enough to suggest an independent stratum of water in neutral equilibrium (sigma-theta = 27.862) and in which the oxygen content increases rapidly with temperature.

Between 3.5° and 4.0° the region of maximum oxygen content occurs; it consists undoubtedly of water of northern origin with a component from the Norwegian Sea. Although the scatter of the oxygen observations is large and defies curve fitting, the few observations of salinity in March and September are fitted by yet another curve lying along an isopycnal, sigma-theta = 27.831.

This highly heterogeneous water around a potential temperature of 3.8° and a depth of 1900 m may be scheduled for intensive study. By using the analogy of the complex geology of the Isle of Anglesey or Mona, such a complex, highly laminated water mass may be called a "Complex" and to distinguish this one from others a name from Celtic folklore, "the Merlin Complex," is appropriate.

Between 5° and 8° the theta/S diagram (Fig. 2), confirming work in earlier years, suggests another water mass in neutral equilibrium (sigma-theta = 27.800), but there may be a slight change in slope of the theta/O_2 curve at about 6°.

Discussion

The usual concept of the deeper water in the eastern North Atlantic is that, in the water below 2000 m and the bottom, there is a small but steady increase in density downwards. This investigation suggests that this view should be reexamined.

It seems that we have a multiple sandwich structure, consisting of a series of layers, each in completely neutral adiabatic equilibrium. For these layers it is possible, by the method of least squares, to calculate straight line relationships between potential temperature and salinity and between potential temperature and oxygen. The changes in temperature and in salinity compensate each other precisely to give potential temperature/salinity curves parallel with the isopycnals. Working up from the bottom we may have adiabatic water masses with potential densities 27.903, 27.892, 27.862, 27.831, 27.800, and conceivably two others at about 27.818 and 27.803 (Fig. 8). If the broad principle presented here should be confirmed, it is not anticipated that these figures will be precisely reproduced. Particularly, may this be so for data obtained with a salinometer.

The curves for neighboring water masses in adiabatic equilibrium do not intersect. Consequently, they may never have been in direct contact, and their areas of formation may need to be sought in quite different places.

These labile well-ordered strata seem to be separated by what were first called zones of conflict. In these zones the density increases with depth, and the oxygen contents are chaotic but usually high. It has not been possible to bring any kind of order into the results. No curve can express them accurately. Our close sampling has not been close enough to reveal any fine structure that the zones of conflict may have. It may not be chance that large dis-

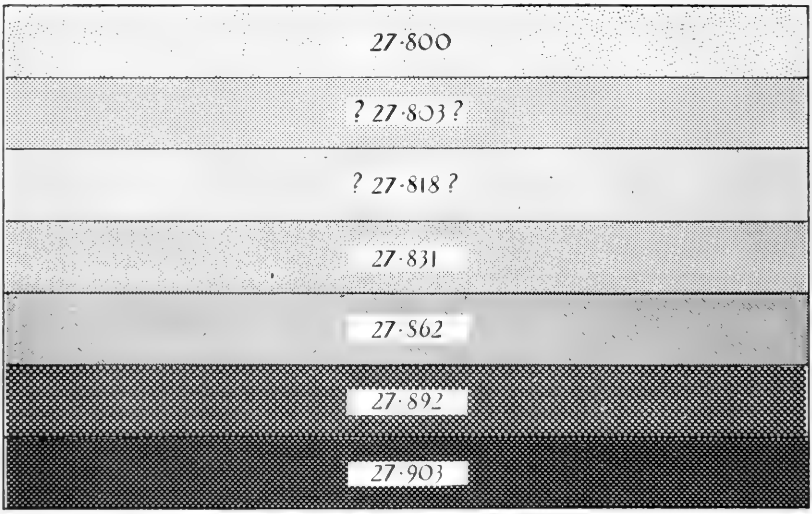

Fig. 8. Resident water masses each in neutral adiabatic equilibrium in the deep waters of the Bay of Biscay below 1400 m depth.

crepancies between replicate oxygen analyses are concentrated in the zones of conflict. They are rare in the water masses in adiabatic equilibrium. This suggests that the zones of conflict are extremely complex and that the boundaries are so sharp that a single water bottle may bring up a sample cut out of two sharply separated layers.

An observation of Revelle *et al.* (1955) is consistent with this description. They labeled deep water with a radioactive marker and observed that it spread laterally in a sheet about a meter thick and extending over an area of 100 or more square kilometers, that is the marker spread outwards along an isopycnal surface.

All advance in deep-sea oceanography, using salinities, depends on interpreting differences not much greater than the errors of measurement. This is so here. An exact measure of statistical significance is not readily made but on a rough assessment the chance that the thesis of this paper might have been derived from data which are, in fact, randomly distributed is about one in twenty, i.e., there is this probability that the whole paper is no more than a canard.

Interpretation

What follows is purely speculative. The layers of water in adiabatic equilibrium are considered as long-term resident waters of the eastern North Atlantic; the zones of conflict contain waters intruding from elsewhere.

Let us consider some hypotheses earlier put forward (Cooper, 1955a,b; 1957). Figure 9 shows schematically boluses of Greenland Sea water which have spilled over the sill of the Denmark Strait into the Atlantic. Similar boluses from the Iceland-Faeroe ridge slipping into the Atlantic along the eastern flank of the Reykjanes and mid-Atlantic ridges are visualized.

The boundaries will not be neatly sharp as necessarily in the picture but will be zones of mixing with the enveloping resident waters. Thus the boluses start as relatively simple affairs, but as

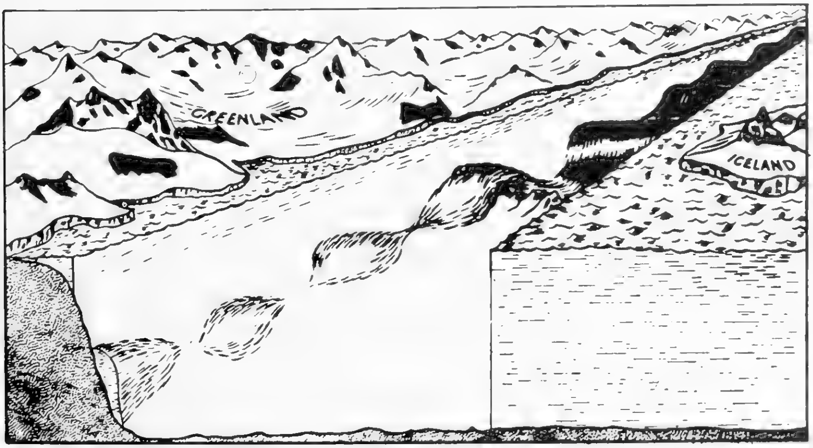

Fig. 9. A speculative, schematic block diagram of the manner of formation of boluses in the Denmark Strait. Much of the water in the main channel is cut away. The internal waves within the Greenland Sea idealize a spectrum of widely variable amplitude, wavelength, and direction. The subsequent descent into the deep Atlantic while pinned against the continental slope of Greenland by the Coriolis force is also illustrated. Submarine canyons dissecting the continental shelf of Greenland may also in part canalize the course of the boluses. The free surfaces of the boluses may respond to irregularities in the rock wall of the Greenland continental slope and may become blurred by mixing with enveloping North Atlantic water.

mixing proceeds they will develop what can only be called a honeycomb structure of pockets of rather varying composition. As time passes and the journey proceeds, the earlier components will tend to homogenize but fresh complexity will become built into the bolus as it descends into deeper and deeper water. Ultimately the bolus will arrive at a level of potential density in the deep ocean equal to its own. It will descend no further.

Some slender evidence that in the deep ocean the resident water consists of a series of plates of different waters each in neutral adiabatic equilibrium at closely defined potential densities has been given. If a bolus has a potential density precisely that of one of the resident water masses, it should quickly amalgamate with this and be lost to sight. The greater probability is that the bolus will have a density somewhere in one of the gaps between the densities of the several resident water masses (Fig. 8); that is, the density discontinuities form a series of platforms at sigma-theta 27.831, 27.862, 27.892, and 27.903. Consequently, a descending bolus will tend to come to rest on one of these platforms where its thickness —as a static system—makes it unstable. It will tend to spread widely in the density gap as a thin plate of water of thickness measured in meters or even centimeters.

No two boluses are likely to have quite the same history. They are not likely all to have the same size when they are born. The mixing history of each is likely to be different. Consequently, not only are they likely to come to rest on different discontinuity platforms but each is likely to have rather different temperature, salinity, and oxygen contents. They will all flatten out to form thin plates of water between the main plates of the resident water masses and show a considerable range in composition (Fig. 10).

These thin plates are likely to differ in density ever so slightly from each other and so would build up into a complex laminated structure occupying the density gap between the resident water masses.

This then is a speculative explanation of the failure to rationalize the data around potential temperatures of 2.5°, 3.1°, and 3.8°. I suggest they represent a situation so complex as to defy the effort we have so far brought to bear on it.

If the thesis is accepted, some riders follow.

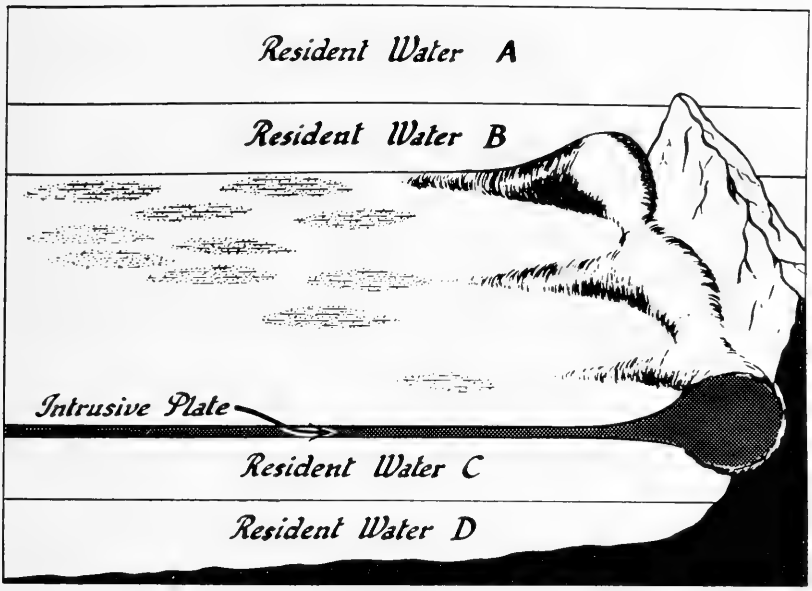

Fig. 10. A solid diagram to illustrate the possible fate of boluses descending the eastern face of the mid-Atlantic ridge or the continental slope of North America. The boluses first come to rest on the discontinuity platform between two resident water masses *B* and *C*, each in adiabatically neutral equilibrium, and then spread out between the resident water masses as thin lamina having lenticular structure.

Neutral Buoyancy Floats

These depend on the relative compressibility of the float and of water (Swallow, 1955). Even in water in neutral adiabatic equilibrium, the density *in situ* increases with depth so that some floats may float within such a water mass. Nevertheless the laminated structure of the deep water may result in many floats coming to rest on the discontinuity platforms. These platforms are likely to have the properties of glide planes with large variations in direction and strength of current within a vertical range of a few meters. Consequently, the use of free floating devices for measuring very deep currents may suffer from restrictions imposed, if the thesis is true, by the very nature of the deep sea.

Furthermore, at these discontinuities, neutral buoyancy devices may, perhaps, bounce about for a while with little hysteresis loss.

Biological Consequences

It is likely to be difficult for any kind of suspended matter with compressibility similar to water to remain long in a stratum of water in neutral adiabatic equilibrium. Such matter will tend to fall to the discontinuity below or to rise to the one above. This means that water masses in neutral adiabatic equilibrium may be very transparent and would carry no food for anything to live on. They may be biological deserts.

At the discontinuities in strong contrast, some of the "rain of food from above" will tend to come to rest. The descent of boluses from the more productive upper layers and their lateral spread at the end of their journey should also intercalate suspended matter into the "zones of conflict" which may be identified with the discontinuity layers. Thus both by vertical and horizontal processes, food is likely to be introduced and held at the discontinuities. It is here that one might expect all deep-sea living organisms to make their living.

An observer descending in a bathyscaphe would pass through a succession of wide transparent, almost azoic layers and, intercalated with these, a succession of thin, relatively turbid water layers rich in animals living on the food chain initiated on the basis of the suspended matter. Bernard (1955), indeed, observed something very like this.

It is more than likely that each discontinuity may provide a rather different biological habitat from the others. It would not be surprising to learn that an observer in a bathyscaphe could identify biological indicator species for each main discontinuity. Many deep-sea pelagic animals are weakly calcified and ill adapted for strong swimming. Many may well spend their whole lives and their offspring may be maintained at one of the discontinuities, never to visit those above and below. The intervening deserts may curb ambition to travel.

On the Age of Water Masses

It seems that the time lapse between birth of a bolus on the ridges between Greenland and Faeroe and its arrival on its appropriate density platform may be a matter only of months. The lateral spread of the thin plates within the zone of conflict is likely to be slower but even so may be a matter of only a few years. In this sense these plates could be said to be very, very young with an age measurable in years on our fingers. Let us consider what C^{14} determinations might show.

The energy for the whole process is provided by a thermodynamic cycle between equator and pole. One step in this cycle is the creation of very heavy water by cooling of saline surface water in the North Polar Basin. It is not established that even here CO_2 is in complete equilibrium between air and water (cf. Broecker *et al.*, p. 301). It is probably more nearly so than anywhere else in the oceanic waters of the Northern Hemisphere. This water then sinks into the deep basin of the Norwegian Sea where it resides for an unknown time. Not again does it attain contact with the atmosphere.

Then as a series of boluses, possibly connected by narrow necks, it escapes into the Atlantic and descends to its appropriate density platform. All the while, the boluses are mixing with enveloping Atlantic water of considerable C^{14} age. By the time the boluses are in a position to spread, their parentage has become very mixed. Our search for an understanding of ocean circulation may be impeded, not helped, by attributing a C^{14} age to water masses such as these. We should be much helped if we could show that the C^{14} content of water of potential density 27.845 was higher than either of the waters of density 27.831 and 27.862. This would mean that the middle water in the sandwich included a proportion of water which had quite recently been at the surface in the Norwegian Sea. We have to remember that the waters of the ocean are mixing, mixing, mixing all the time and that we have to train our resources upon situations where these mixing processes can be unraveled. To consider, as an end in itself, the integrated age of a water mass which has been created by a succession of mixing processes is to miss the point.

Fisheries Hydrography

Now let us consider an application to fisheries hydrography. A hypothesis that the success of the fisheries of the continental shelves of northwestern Europe depends on the succession of cold and mild Arctic winters has already been published. The chain of reasoning goes through the deep Atlantic. The argument halfway through splits into two components which are complementary. The work here provides missing links for both.

There remained a gap from well down the Reykjanes ridge to the Bay of Biscay which has proved very difficult to bridge. There have been dynamic objections to every tentative theory. These now vanish. There seems no difficulty in accepting the spread of a laminated complex of bolus-derived waters in any direction along the glide planes between the several resident water masses each of which is in neutral adiabatic equilibrium.

These glide planes would also provide the channels to conduct internal waves across the Atlantic from the sinking boluses along the mid-Atlantic ridge which create them to the slopes of western Europe where they can create turbulent mixing and ultimate enrichment of the shallow waters with nutrients.

If the thesis of this paper can be more firmly established, the study begun in 1946 will have been completed.

For the future of fisheries hydrography, if we can follow the variations in thickness of the zones of conflict, i.e., obtain a measure of the volume of bolus water entering the eastern North Atlantic, we have an overall measure of the potential productivity of the shallow seas of northwestern Europe. Very intensive study of a few fixed stations like our station Cavall to 4000 m depth, perhaps no more than one, may enable us to do this.

Charting the Distribution of the Water Masses and Complexes

The interpretation presented here is for a single position in the Bay of Biscay. It should be possible to recognize the continuity of each water mass over a wide area of the eastern North Atlantic, to follow any gradual change in properties, and to seek for the source where each has been created. If the general picture can be confirmed, its extension will need very precise and time-consuming work not readily compatible with the usual pattern of deep-sea expeditions. A limited aim attacked by an experimental approach may more quickly and surely provide an answer.

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MARY SEARS

30 March 1961

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