

CHAPTER V

LIFE IN THE SEA

DIFFERENCES, in the disciplines employed, and in the nature of the immediate problems attacked, make it convenient to classify this branch of science under three headings: (1) Oceanic Zoölogy and Botany, (2) Marine Physiology, (3) Marine Bacteriology.

The first of these is chiefly concerned with the ways in which the basic conditions of life in the sea are made manifest by the diversity in structure and in habits of animals and plants. This includes such subjects as taxonomy and its relation to geographic and bathymetric distribution; the dependence of successful reproduction, growth, migrations, and so forth, on definite factors in the marine environment, embracing also the general subject of life histories; the adaptations that enable various groups to populate particular parts of the sea; the interdependences of different species of animals, and of animals as a group on plants; the environmental factors that govern plant growth; and all problems in cognate fields.

Marine physiology covers the study of the general and basic conditions and phenomena of life that are common to marine animals and plants; of the vital reactions between the cell, or aggregate of cells, and the external environment; of the interactions be-

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tween the various tissues and the blood or lymph; also of the physiological adaptations of unicellular and multicellular organisms to variations in the sea-water environment.

The heading 'Marine Bacteriology' covers all the activities of bacteria in the sea.

1. OCEANIC ZOOLOGY AND BOTANY

These headings cover the same fields of study in the sea as do the corresponding sciences on land; hence students have precisely the same reasons for pursuing the former as the latter. Consideration of the characteristic differences between marine and terrestrial life likewise makes it clear that the pursuit of oceanic zoölogy and botany, as contrasted with terrestrial, also opens certain special avenues for the general advance of biology.

There would be ample justification for pursuing the marine branches of the sciences in question from the descriptive standpoint alone, if from no other, to increase our knowledge of the kinds of animals and plants that exist upon this planet. For it is certain that a formidable proportion of the inhabitants of the sea (i.e., two thirds of the earth's surface) still remain to be discovered, while our knowledge of many others that have already been found is far from complete even as to their structure, let alone their activities. And as long as new animals are to be found, we

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may be sure the biologist will seek their discovery, for he dare neglect no opportunity to explore the actual manifestations of life, whether by land or by sea. Collecting expeditions at sea are therefore urgently needed, especially along the less frequented coasts, and in the mid- and abyssal ocean basins; in this way rich harvests of fishes, crustaceans, mollusks, and so forth, never before seen, are brought to light from time to time. Hand in hand with field work of this sort must go the study (in museums ashore) of the collections so gathered.

The situation in this respect is on precisely the same plane in the sea as it is on land, where the need of fresh collections from little known regions, to enlarge our knowledge of birds, reptiles, or of insects, is so commonly appreciated that it is not difficult to obtain support for such undertakings. It is only because the variety and beauty of the fishes, crustaceans, and other groups of animals in the oceans, and the interest that attaches to their life histories, are appreciated by so few that it is not equally easy to find support for collecting expeditions for them. All of which applies equally in the case of oceanic plants.

At the present time much attention is being paid to the geographical distribution of the marine inhabitants, with reference, for example, to the latitude, to the strength of the sunlight, and to the tem-

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perature, for we still fall far short of an adequate knowledge even of the broad outlines of such matters. The problems that may here be grouped are not easy either of definition or of solution if we attempt to advance beyond the primary descriptive stage, while as yet we have hardly entered even into this introductory phase in the case of most of them.

This applies even to the horizontal distribution of marine animals and plants — the aspect of the general geographic problem that is most readily attacked — because serious gaps in the faunal mosaic still remain to be filled in for extensive sectors, of coastline as well as of sea bottom. As taxonomic studies become more and more critical it proves that many of the identifications of the past, on which generalizations as to the faunal relationships of different areas have been based, must be revised. And this whole field of study is vastly complicated by the involuntary migrations to which so many marine animals and plants are subject, and by which whole communities may be (and often are) carried to regions which they cannot permanently colonize. A case in point — perhaps the best known example of broad scale transport to unfavorable regions — is that of tropical pelagic organisms to fatally high latitudes by the agency of the Gulf Stream. And every gradation is to be seen in this respect, from sporadic drifts, of occasional individuals, far outside

their normal ranges, to the opposite extreme where a supply is so constantly brought from some far-off source that a permanent community is mechanically maintained in parts of the sea where the species in question cannot reproduce themselves. A familiar example of the latter category is afforded by certain pelagic worms in the Gulf of Maine; perhaps also by the rosefish (*Sebastes*) around the coast of Greenland.

In this connection one's thoughts turn, naturally, to the series of problems that group around the bathymetric distribution of the animals and plants of the deeper zones of the oceans in different regions, at different times of the year, and at different times of day, for discoveries recently announced suggest that some of the views currently held are incorrect. And the differences in habit between adults and young in many cases (perhaps in all) added to the differences at different latitudes, so complicate this whole field that the correct description which must precede any sound analysis still lies far in the future.

Perhaps in no phase of oceanic biology would advances be more welcome than in that concerning the whole question of the productivity of the sea under the conditions that actually exist at different times and places, and of the factors that control the amount of organic production that does in fact take place. The obstacle to advance in this field has not

laid in any failure to appreciate its importance: on the contrary the literature on this subject has grown to formidable dimensions, while numberless counts of diatoms, copepods, fish eggs, and other things have been made — also enumerations of organisms of one sort or another living on given areas of the sea bottom in various regions. But it has proved so difficult to devise technique that would be comparable for different times, for different places, and for different groups of animals, that no really adequate method of general attack has yet been found: even to measure a thing apparently as simple as the volume of organic matter present in the water at a given time or place. Nor are counts of individuals comparable except in the rarest cases, because different stages in growth (different sizes) are involved.

Inseparable from the general question of the abundance of marine life is that of the factors and events that control the success of organic production. The question, what is responsible for the wide variation between good and poor years of production for various fishes, is very much to the fore at present in fisheries biology. As this is discussed on page 217, we need only remark here that the same problems arise in connection with every marine animal or plant, and that our knowledge in this whole field is still practically *nil*. As yet we know little of the interrelationships of different species or

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groups of animals in the sea beyond the obvious fact that some prey upon others, but we may be certain that in many cases interrelationships of less obvious sorts are vital links in animal economy. And it would be as easy to multiply this list of urgent biologic problems for the sea as for the land; as impossible to make a complete enumeration, for even if one could conceive of such a list as covering the field today, every advance in knowledge would open new vistas that one cannot now foresee.

Among the more special reasons for encouraging marine zoölogy and botany, as contrasted with terrestrial, one might first mention that of convenience. It is, in fact, safe to assume that this, of itself, would be reason enough for biologists constantly to turn to the sea in the future, as they have in the past, for subjects of investigation, whether in surveys of the gamut of animal form or for the study of particular problems in the various fields of morphology, ecology, and so forth.

The fact that the ocean is the home of the oldest and simplest types of various phyla, that it supports representatives of every phylum, and that it is the exclusive home of at least one of the latter¹ explains why the comparative anatomist requires access to marine organisms. The comparative embryologist

¹ Of a second, also, if the ctenophores be considered a separate phylum.

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profits for the same reason; for him certain marine forms — selachians, echinoderms, ctenophores, and many others — are classic material. For work in experimental embryology, the eggs of echinoderms, nemerteans, certain marine annelids, mollusks, and fishes are especially adapted both because they can be obtained in unlimited quantities, and because the fact that they are laid and will develop in sea water over considerable ranges of temperature makes them suitable for experimental procedure. Contrast this with the scarcity in number and inaccessibility to experiment of the eggs of mammals. Except in the water, furthermore, no eggs are laid without extraneous protective devices.

The student of egg-cleavage, cell-lineage, and allied subjects has benefited accordingly by the favorable subjects afforded by marine animals in the past, and it is certain that the embryologist of the future will similarly benefit as new lines of attack open in his particular province. In the same way the abundance of life along the seashore offers particular advantages to the student of ecology; as, for example, through the opportunity that is open for the investigation of highly complex colonial developments, and manifestations of the divisions of labor among lowly organized groups in the sea. It is, in fact, the unique opportunity for biological studies in many and diverse fields offered by various marine

organisms which has led to the establishment of the marine biological stations that have played so large a part in the modern development of theoretical as well as of observational biology in general.

It would be easy enough greatly to extend the foregoing statement of concrete problems that face the zoölogist or botanist in the sea, and of the directly practical reasons why biologists in general should turn to marine organisms, were there any need of so doing. The chief purpose of this chapter is, however, to show how differences between the conditions of life in the sea and on land open roads along which oceanic and terrestrial biologists can advance toward their common goal from somewhat different angles, allowing the convergent approach that has often been productive in science in the past. We refer to the simplicity, constancy, uniformity in time as well as in space, and favorability as an environment for living substance as constituted on this planet, of sea water as contrasted with air. Thanks to these characteristics, we may hope to trace the underlying relationship between the living plant or animal and its physical-chemical surroundings, as well as between different groups of organisms, in a more direct way in the sea than is usually, if ever, possible on land. In many respects, therefore, the former is the more favorable natural laboratory of the two, for

investigations into the underlying principles that govern animal and plant ecology.

Certain of these peculiarities of the sea as a home for life have often been signalized of late. But a re-statement here is called for, to justify the thesis just set forth.

The most obvious advantage of the sea water, contrasted with air as the home for a substance (proto-plasm) composed chiefly of water, is that it is an aqueous solution. The physiologic-morphologic bearing of this fact, with the resulting contrast between all terrestrial organisms on the one hand and all aquatic plants and animals (sea or fresh water) on the other, is as obvious as it is direct. All animals and plants in the sea being free from the water-needing complex by which every animal and plant living in air is bound, none needs or has developed any of the protective adaptations which their relatives on land have been forced to elaborate in order to guard against the failure in the supply of metabolic water which, for them, is apt to be fatal, even if of the briefest. We see nothing, for example, in the sea in any way comparable to the storage of water by the stomach of a camel or in the stems and leaves of certain desert plants. Neither is it necessary for the external covering of any aquatic organism to serve it as the protection against a loss of water from inside the body to outside, which is the one absolutely essential

function of bark, rind, skin, and so forth, on land. Freed from this compelling factor, living substance may (as one contributor to this report has pointed out) even remain naked in the sea, which is never possible in the air: or if it cover its outer surface with a skeleton, it may employ a great variety of materials; lime, silica or even strontium, cellulose, agar, chitin and spongin, as well as solidified proteins.

Equally direct, though perhaps less obvious, is the relationship between water and the geographic distribution of marine as compared with terrestrial animals, all parts of the sea being equally open to all living creatures, so far as this factor is concerned. Contrast this with the state existing on land where it is a commonplace of schoolboy instruction that the supply of drinking-water, together with the dampness of the air, largely controls the kinds of animals or plants that can inhabit different regions of the earth.

Still further simplicity of metabolism is made possible for marine organisms by the thermal uniformity of the medium in which they live, as contrasted with their relatives on land, which must (by and large) be able to accommodate themselves to wide and rapid variations in the temperature of their own bodies (because temperature controls the rate of so many chemical reactions) or else must be able to guard themselves against such changes. It is com-

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mon knowledge that the activities of animals and plants of the first of these two categories (i.e., those with internal temperature nearly the same as that of the surrounding air) are greatly limited in regions where the temperature range of the air is wide from hour to hour, from day to day, or from season to season. A familiar example is the sluggishness of snakes, turtles, and so forth, and of many insects, in cold weather as contrasted with their activity in warm. And while the maintenance of an even body temperature (actually a high one) independent of the temperature of the surroundings does not necessarily require any general modification of the gross anatomy, it does involve metabolic adjustments so delicate that any disturbance of the regularity of its control is apt to be fatal. It also requires that the surface of the body be in some way insulated against the passage of heat, as by the fur of mammals, the feathers of birds.

Marine life is free from the need of such thermal adaptations and protections because the changes in temperature at any given place in the sea average not only very much smaller than they do in the air, but very much slower. Throughout most of the ocean deeps, in fact, the temperature is practically unvarying from year's end to year's end. And while shoal waters in high latitudes do show considerable alterations in this respect with the change of the

seasons, it is only close to the surface that such changes are great. Consequently, any animal can reach a nearly constant thermal environment even there, merely by swimming down a few fathoms to avoid extremes of summer heat or of winter cold, as many fishes actually do in their regular bathic migrations.

On the whole, therefore, marine animals have not found it necessary to provide the specific protection against thermal variations in the environment that is provided by a self-controlled body temperature. That is to say, the discovery of warm blood has never been made in the sea. All the warm-blooded animals that now live there, whales, seals, walrus, and so forth, are descended from warm-blooded terrestrial ancestors. And in maintaining their body temperatures these marine mammals not only enjoy no advantage but are under a positive handicap because the high thermal capacity of the surrounding water makes this a much more difficult task for them than it is in the air. It is to meet the resultant problem of insulation that seals as well as whales are enclosed in their envelopes of blubber; bulk that is of no direct service except as protection against outside cold, but is in other ways actually detrimental because its presence requires more food and increases the difficulty of propelling the body through the water. Contrast with this the happy condition of the

fish which needs fat not at all for the purpose of insulation, but only as a storehouse for energy that can be drawn on even to the point of total exhaustion if famine so require.

Judged from the standpoints of numerical abundance and ability to people all parts of the sea, marine mammals as a group have not been as successful as the fishes, although both the metabolic activity and the thermodynamic efficiency of the organism as a whole are far higher in warm-blooded than in cold-blooded animals.

It is because of the thermal constancy of the sea water that marine animals as a whole, whose internal temperatures are practically those of their surroundings, rising and falling as the latter rises and falls, do not pass through the alternating periods of activity and stagnation that on land are characteristic of cold-blooded animals, except those of the tropics. In the sea, as a general rule, each species is attuned to a certain optimum range of temperature in which it passes most of its life, but within which range various phases of its vital activities, especially of its reproduction, are directly controlled by temperature changes. Otherwise expressed, cold-water fishes may be as active as warm — witness the trouts and salmons or the herrings. When, as sometimes happens, a sudden change in the temperature causes widespread destruction (page 72), Nature's provi-

sion for the reëstablishment of the species in the sea is simple, being merely a production of many more eggs and young than can survive under normal conditions.

These thermal differences between the aquatic and the terrestrial environment make the study of the relationships that the activities of the organism on the whole (as distinguished from its several constituent tissues) bear to temperature far simpler among marine or fresh water than among land animals. And the control that temperature exerts over the life processes makes this a very important subject in relation to such questions as geographic and bathymetric distribution, migrations, breeding seasons, and rates of growth, to mention but a few.

The comparative opacity of sea water to solar radiation, especially to the part of the spectrum that carries most of its energy, protects all of the inhabitants of the sea, except such as live close to the surface, from the lethal effects of sunlight, thus freeing them from the need of developing any opaque covering for protection from the sunburn against which every terrestrial animal must in some way guard its living substance. Because of the resultant rapid gradation in the strength of the light from the surface of the sea downward, and because of the ability of marine animals to escape light by sinking, the sea, therefore, offers a far better opportunity than

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does the land to study the whole category of tropisms caused by light stimulation; also the natural economy of animals that live permanently in total darkness as well as the problems that center about animal luminescence.

This applies equally to the study of pigmentation, because one of the chief factors that controls its development among land animals — light — plays so much less important a rôle in the sea, allowing pigment the more directly to reflect internal metabolic activities there. A case in point is the fact that while animals living in darkness on land are usually colorless, those of the ocean abyss, below the influence of the sun's visible rays, are usually intensely pigmented, often a velvety black, a difference reflecting in the one case a loss of pigment previously developed by ancestors that lived in sunlight, in the other case the development of pigment untrammeled by light, its causes as yet unknown.

Another contrast having far-reaching biologic effects is that between the specific gravity of the medium in which organisms live on land — the air — and in the sea. Thanks to the fact that sea water has almost the same specific gravity as protoplasm (or protoplasm as sea water if one prefer) no marine animal or plant needs the mechanical support against the pull of gravity that every organism of any considerable size must have on land if it is not to col-

lapse of its own weight. Thus no alga needs, or has developed, a rigid woody skeleton. And as marine animals have never required strong frameworks to support themselves, their internal or external skeletons can be adapted entirely to other ends, such as protection (as in the case of many mollusks) to provide stiffness as among the horny corals, to maintain body form against resistance of the water while swimming or for the attachment of muscles as among fishes and crustaceans. Comparison of the frame of a whale (which suffocates of its own weight if left stranded on the beach by the ebbing tide) with that of an elephant or a dinosaur shows at a glance how much less is necessary in the one case than in the other. In spite of their great muscular power, even the largest sharks have still feebler and wholly cartilaginous skeletons without any hard bones, while even a more striking case of strength without framework is afforded by the giant squids, animals proverbially active, swift and muscular, though with only the rudiment of any sort of skeleton. No morphological development of this sort would be possible on land. As a corollary of this, there is no gravitational limit to the size of animals in the sea, the only theoretic limit being their need of taking in, through the surface (and usually through a very small part of it), enough food to support the entire bulk and enough oxygen for its vital requirements. With this

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relief from the force of gravity, the sea supports animals as large today as it ever has, and heavier than any that have existed on land.

Freedom from the need of supporting columns also relieves marine animals of a factor in form-regulation that is one of the most potent and wide-working on land, but which may justly be termed adventitious because it is not inherent in the nature of living matter, nor in an environment essentially favorable. We refer to the fact that animals in the sea have no basic necessity of arranging their limbs as supports — they may or may not carry these on their lower surface. And the contrast in this general respect between land and sea animals is apparent in many other ways.

The high specific gravity of the sea water also exerts another very important, as well as universal influence on the lives of its inhabitants, because coupled with the fact that it is at the same time a nearly perfect fluid, i.e., highly mobile and in constant motion. Through this combination of physical characteristics a mechanism for suspension combined with transportation is constantly at work in all parts of the sea. As a result we see the zone that is permanently habitable extending there to three dimensions, its thickness equaling the extreme depth of the ocean, whereas on land it reaches upwards only to the tops of the highest trees, downward a few

feet into the soil. This allows whole categories of animals and plants, with which science has been much concerned of late, to pass their lives swimming or drifting suspended midway between surface and bottom, an ecologic community that has no true parallel on land, its closest analogy the spiders, insects, and seeds and spores of plants that are borne by the wind.

In this purely mechanical way the problems of transportation and dispersal are solved for multitudes of these drifting creatures (the plankton), assuring the dissemination of whole groups of species in the sea without directive swimming on their own parts. And even many fishes benefit (as species) thereby during their egg and larval stages, or suffer correspondingly if carried to unfavorable regions.

The group-benefits conferred by this involuntary transportation are numerous, even though to the individual it may be fatal. Thus the dissemination of species from the centers of chief production, just mentioned, is assured; in many cases a matter of prime importance for their survival. The problems of reproduction are also vastly simplified thereby, for provided eggs and sperm be produced simultaneously and in sufficient quantity, a means is provided ready-made for bringing the two into contact, without effort on the part of the individuals concerned. And correlated therewith we find that

the development of peculiar mechanisms for this end — the rule among land animals and the higher land plants — is decidedly the exception in the sea, freedom from this necessity being reflected by corresponding morphological simplicity.

The water of the sea, by its constant motion, and by carrying a vast assemblage of living things with it, also provides a much more effective mechanical mechanism for bringing food within the reach of animals that are stationary than ever works on a broad scale on land. And as a wide variety of animals in the sea need merely await what the current brings them, the ability to carry out self-directed locomotion is not the basic necessity there, even for carnivorous animals, that it is on land. In fact, whole categories of flesh-eaters — even eaters of active prey — manage very well in the sea without it, and all gradations are to be seen there from animals that swim or crawl actively at some stage in their life, through such as do so for a time (then becoming stationary as the barnacles and corals) to others that are stationary, or nearly so, from birth to death, such as the stalked crinoids. If density of aggregation or numerical strength in individuals be an index to success in the struggle for existence, the oysters, mussels, and so forth, the deep-sea crinoids, the reef corals, and the sponges find a stationary life highly successful. And this applies even to some ani-

mals of considerable size, such as the giant clams (*Tridacna*) of the coral reefs.

Thus while most groups of animals in the sea, as on land, have been controlled in their structural evolution by adaptations for locomotion, such as streamlined bodies easy to drive through the water, many others show no effect of this in their form regulation. Such animals teach us, for example, that the possession of lateral limbs, or of the bilateral symmetry with which we are so familiar that we have almost come to look on them as necessary features of a 'higher' animal, is actually not a basic animal necessity at all, but merely adaptation to a particular environment or way of life.

The high specific gravity of water, the fact that it is an aqueous solution, its comparatively constant temperature, the protection that a very thin film of it gives against sunlight, and its incessant motion, combine to make the whole problem of reproduction much simpler for marine, than for terrestrial animals. Eggs need less protection, and the young hatched therefrom are capable of independent existence at an earlier state in development than is the rule on land. So we find that even the most highly organized of the animals of direct marine ancestry (the bony fishes) solve the reproductive problem as a group merely by producing a great many eggs, without any complex arrangements for nursing the

latter, or caring for the young, while larval development is much more usual in the sea than on land. It is true that some fishes (notably the sharks) are viviparous; but judged by the usual criteria this does not seem to have been of any great advantage in group-evolution in the ocean.

The cases so far quoted are enough to show how much more intimately marine organisms (needing no specific protections against the medium in which they live because this is essentially a favorable environment, hence having in most cases developed none) are dependent upon their surroundings, but at the same time far more at the mercy of the latter than are most animals and plants on land. And because responses in structure, in evolution, and in habits, to variations in the environment, are not obscured there by all the variety of protective devices that are developed on land, the sea offers by far the more favorable field for investigations into these subjects.

The peculiar advantages which the oceanic biologist enjoys as contrasted with his terrestrial confrère may, then, be summed up in the one word 'simplicity.' And thanks to this simplicity, we come more easily to grips in the sea with such basic life processes of protoplasm as its incorporation within itself of materials from outside, its growth, and its reproduction.

Similar advantages also apply, in considerable degree, to the investigation of the mental as well as of the physical attributes of marine animals, for, as a corollary to the freedom that these enjoy from some of the most serious difficulties that beset land animals, even the most highly organized of them show a low degree of mentality. Thus there is nothing among the crustaceans comparable to the social systems that some of their insect relatives (ants, bees, termites, and so forth) have elaborated. Nor do any of the fishes of the sea show anything of social organization beyond such rudiments as the tendency of schools to hold together in their wanderings. The animal psychologist thus has at his command in the sea an excellent opportunity to examine what may be called the basic mental processes of a great variety of animals comparatively high in the evolutionary scale, unobscured by the confusing psychic developments that have been stimulated on land by the struggle to survive in spite of harsh surroundings. The problems of large-scale behavior, for instance, as illustrated by the phenomena of schooling, can be studied to best advantage in the sea because they can most clearly be seen there. And the uniformity of the surroundings in which marine animals live makes the sea a far more promising environment than is the land for researches into the stimuli or receptive senses responsible for the so-called 'volun-

tary' migrations. It is still a mystery how fishes and other marine animals are able to direct their long journeys, often in darkness, and always through a medium in which temperature and chemical composition are so nearly uniform over long distances that the most delicate tests are needed to reveal any difference at points many miles apart. The problem here is akin to that of bird-migration, but an even more puzzling one.

The essential difference between the paths of study which may be expected to lead terrestrial and oceanic biologists most directly toward their common but perhaps unattainable goal — solution of the nature of life — may therefore be contrasted as follows. The former studies most profitably the manifold adaptations which animals and plants have evolved to make an unfavorable environment serve their ends: adaptations whether of structure as examined by the morphologist and the taxonomist, of development as seen by the embryologist, of mental processes, or of the internal vital phenomena that fall within the province of the physiologist as discussed in the next chapter. For the oceanic zoologist or botanist, however, the most productive subjects group around the animal and plant forms, life histories, and so forth, that have developed, free on the one hand from the stimulation and on the other free of the limitations that are imposed on terrestrial

organisms by the necessity of guarding against their surroundings.

Oceanic zoölogy and botany also render invaluable service as handmaidens to other provinces of sea science, because biological phases are inherent in many of the problems of marine geology, physics, chemistry, and so forth. As this interrelationship is emphasized repeatedly in other chapters of this book only a few examples need be quoted here. One thinks perhaps first of the geologist's need for information about the regional abundance, specific distribution, migrations, death-rate, rate of sinking after death, and details of skeletal formation of all the categories of animals and plants whose limy or silicious remains form so large a part of the deep-sea oozes. The pelagic shell-bearing Foraminifera and Radiolaria demand attention in this connection no less than the diatoms which have been the subject of so much investigation of late. Ability correctly to interpret the accumulation of organic oozes today, or in the past, depends upon such knowledge, which applies equally to all the problems that center around the building of reefs from the remains of bottom-dwelling animals — coral reefs, for example — and the origin of shell beaches. The geologist is no less interested in corresponding problems regarding the various mud-eaters that live on the bottom of the sea, because of the destruction (chemical and

mechanical) of existing sediments that they bring about; the rôle which such animals may play in keeping open the lagoons of coral atolls is now under discussion. Knowledge of oceanic biology is equally vital for the palaeontologist; he cannot hope correctly to interpret the fossil record in time or space, or the animals of the past, without a much more detailed knowledge than is yet available of the distribution and conditions of life of the animals and plants of the sea, because the great majority of all the species of animals whose fossil remains have yet been found certainly lived in the water, either sea or fresh.

It would be equally futile to attempt any explanation of the cycle of chemical events that is constantly proceeding in the sea without taking into consideration their biologic aspects: in fact it is often impossible to say which of these categories of events is mistress, which handmaiden. Thus it would be idle to discuss the increase and decrease of various chemical solutes in the sea water without knowing something about the decreases and increases in the plant communities that precede or accompany them, because these plants contribute materials to the water on the one hand and on the other hand withdraw other materials from the solution. This applies exactly in the same way to the problems of the lime chemistry, of the alkalinity, and of the gas con-

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tent of the water. And as different organic groups are laws unto themselves, the lives of many of them must be examined intimately in these connections.

Students of ocean currents can and have drawn much valuable information as to the sources and directions of flow of different water masses from the animals and plants that the latter carry with them, depending upon the biologist to tell the thermal relationships and probable geographic sources of these natural drift-buoys. And in this case the negative evidence afforded by the absence of particular communities of species may be hardly less instructive than the positive evidence afforded by the presence of certain others.

Oceanic biology also has an important and direct economic bearing discussed in another chapter of this report (page 187).

2. MARINE PHYSIOLOGY

The general physiologist, whether he works with marine, with terrestrial, or with fresh-water animals, seeks a better understanding of the life processes that are common to all animals and plants, and of the ways in which the basic properties of protoplasm are translated into the complex manifestations of animal and plant life that we see about us. Hence in the words of one contributor, 'Marine physiology is not so much a department of marine

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biology as a method of dealing with the whole of that field, in so far as it concerns the properties and relations of living organisms, and parts of living organisms.' Physiologists, therefore, turn to marine organisms in their researches for much the same reasons as do other biologists. And they have the same two specially compelling inducements for so doing; first the abundance, availability, and suitability for experiment of marine animals; second the nature of the sea water environment.

The practical advantages that marine organisms offer this branch of biology call first for emphasis because it is not generally recognized how greatly general physiology has been indebted to them for progress in some of its most basic problems. This applies, in particular, to investigations into such energy relations as involve: (1) temperature, (2) light, (3) gravitation, (4) ionic composition of the medium, for which they afford material on which experimentation can be carried out on a large scale, under conditions where no irreversible changes are induced. Marine animals and plants likewise offer the most favorable opportunity for directly relating the experimental results gained in such fields to the phenomena that actually occur in nature, through study of the physiological adaptations to variations in the sea water environment.

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most obvious, we know very well that the distribution of marine animals and plants, in fact their whole economy, is largely controlled by temperature. All of them have an optimum range within which they live, with lethal limits above and below. But in many cases the vegetative metabolic activities (expressed as growth) and the reproductive proceed most successfully at different temperatures — witness the growth of the lobster to large size in cold water, but the inability of its larvae to survive at all except in warm. The question how this temperature control works on the internal activities is now to the fore. Is this a simple matter of difference in the rates of the chemical reactions involved (for certainly the metabolic rates do vary with temperature) or is something more at work? And if well-defined critical temperatures do exist, as has been indicated both by certain field observations and by experiments, how do these influence the distribution, the seasonal activities, and the host of other phenomena that are controlled in greater or less degree by temperature?

Studies of the effect of temperature on the respiratory processes of various marine animals in particular offer a fertile field, and a very attractive one, because this effect is great enough to render tissues that are adapted to the exercise of respiratory functions (i.e., to the transport of oxygen) at one temperature quite worthless in this respect at another, no matter how

much oxygen there may be dissolved in the water. A study of the temperature factor in this relation may to some extent contribute to an understanding of the thermal control of geographical distribution. May this, for example, be one cause of the great differences in thermal requirements between closely related species — or between geographical races of a given species, such as we know to exist among the codfish and the herring, which find their optimum at one temperature in one region, at another temperature in another? In the straits of Belle Isle, for example, the cod prefer and seek much lower temperatures than they do on Nantucket Shoals.

The temperature problem is not only one of the most important in vital economy, but has the added advantage (from the practical standpoint) that this is a convenient factor with which to work, being easily controlled under experimental conditions, while the effects are readily measured.

The specific properties of the respiratory proteins as determinants of the pressure of oxygen gas in the blood are also intriguing in this connection, for the whole question of the oxygen requirements of different animals and of the same animals at different temperatures is little understood. What, for instance, is the physiologic difference between the blood of active fishes and mollusks, such as mackerel and squid, and that of their more sluggish relatives,

and between the tissues that perform respiration among animals with different thermal optima that have no blood, but take in oxygen directly through their epithelial surfaces — the coelenterates, for example? Very little, too, is known about the respiration of the marine mammals; sundry interesting problems spring to mind in this connection.

The basic nature of the respiratory pigments — any pigment, for that matter — has hardly been touched as yet from the standpoint of specific differences within a given group of animals, or of the qualities with respect to oxygen of the compounds, that in lower animals are analogous to haemoglobin in the higher. It is not unreasonable to hope that knowledge, here, may lead to better understanding of the blood physiology of mammals, and so of man. Crustacea, worms, and fishes, among marine animals, lend themselves more readily to investigation in this connection than do any land animals. And respiratory pigments are only one of a great number of substances that cry for study from this point of view. In fact, the whole relationship between chemical composition and systematic relationships among different groups of animals and plants is still a practically virgin field; one offering fertile possibilities to the marine physiologist.

Various other comparative studies which can most favorably be carried out on sea animals, might also

Life in the Sea

prove of assistance to the human physiologist in his attempts to interpret the phenomena he has to deal with. Especially interesting in this field is the occurrence in mammalian blood of salts in proportion similar to sea water, with the contrasting fact that while the body fluids of sea fishes are nearly the same as sea water in this respect, they are never precisely so. The whole question of the physiological significance of the different salts is, in fact, a most important one, to explain which no satisfactory theoretic basis has yet been arrived at. Here new lines of attack are opened by recent advances in the physical-chemistry of salt solutions, for which marine animals, because of their simplicity, are the most promising subjects.

Salts

We have selected these particular fields of study for mention as illustrations of the desirability of applying the methods now practiced in the investigations of the respiratory, circulatory, and blood physiology of man to the comparative physiology of marine animals to a much greater extent than has yet been attempted. An eminent physiologist, indeed, gives it as his opinion that this is one of the great scientific opportunities of the coming half-century; and that voyages of well-equipped expeditions, making use of experimental methods of this kind, promise to put the natural history of the sea on a new level.

*field
Exps*

swim bladder

Oceanography

Hall

In like manner, the key to the riddle of the secretion of gas, over which there has been much controversy in the field of pulmonary respiration, may well be found in the physiology of the swim bladder of fishes, about which little is yet known with certainty. Many questions of nutrition, such as might well be attacked in marine animals, would also find application in the physiology of the higher animals — so, too, the manner of excretion of waste products by the animal groups that have no special organs for that purpose. This, for example, would include the intra-cellular pigments and the crystalline secretions of medusæ.

Calcium metabolism, as reflected by the deposition of lime salts in bones, is another field on which studies in marine physiology might throw much light. Thus the relation between ocean temperature, the occurrence of lime-secreting animals, and the amount of lime they secrete, suggests the importance of investigations into the rôle played in calcium secretion by the effect that other electrolytes may have on the solubility of calcium carbonate.

Fertile subjects in the whole field of the physiology of light are to be found among the great variety of marine animals of widely divergent groups that live normally in regions of very dim light, or of darkness, and so may not have developed an adaptive physiologic protection against the lethal or other meta-

*(no) blenni
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How marine
inland or fresh water*

Ocean vs Lakes (freshwater) as to Variability

Life in the Sea

bolic effects of the whole of the sun's spectrum, or of any part of the latter. This in turn, leads to the very interesting problem of luminescence, so highly developed among marine animals. Furthermore the light tropisms of species attuned to a higher degree of illumination, are more easily studied on marine than on land animals. And this applies even more strongly to geotropism.

light

Many other significant matters might also be approached through the physiology of the animals that live in the depths of the oceans, under conditions very different from those prevailing near the surface, if they could be controlled in the laboratory, which has never been possible so far.

The activities of individual marine organisms, especially those of the littoral zone, likewise provide the widest variety of subjects.

Very attractive opportunities are open for researches concerning the many shoal-water animals that are of commercial importance, the sane conservation of which depends upon knowledge of life history. And the incentive to put such matters on a sound basis is strong, for much of the work so far attempted in this field has failed to command full confidence, both because of the technical procedure employed, and because of the character of the result sought.

Physiology, furthermore, is concerned, not only

with the activities of individual animals or plants, both as such, and as they illuminate specific problems, but also with the inter-connected activities, and ecology in general, of different organic groups. The sea offers the readiest subjects for such investigations, and those likely to provide results of the widest significance.

The investigation of abstract problems, in all these fields, requires, in the first place, the selection of the type of organism that seems the most likely to prove suitable for the specific question in hand. For this reason, alone, if for no other, the marine biological laboratories should expand their functions as foci for physiological research, since by contrast with the faunal and floral equipment of the land, or of fresh waters, the sea is extremely rich, both as to individual numbers and as to variety of types. Here, for example, we think of the abundance and diversity of luminous forms in the sea contrasted with their paucity on land and practical absence in fresh water; of the wide range of colonial animals; of the expression of types of symmetry other than the bilateral; and of various forms of appendages, and so forth, among the marine population. And when we turn to cellular physiology, we find that the large size, abundance, constancy of physiological condition, and simple cultural requirements of such free-living cells as the eggs of sea

urchins and starfish, among others, make them incomparable material. This is true whether surface processes or internal colloidal phenomena be in question, and whether studied by temperature variations, by chemical means, or by microdissection. It was, therefore, no accident that general physiology in America arose at the Marine Biological Laboratory at Woods Hole, or that the pioneer studies in artificial parthenogenesis, of balanced solutions, and so forth, were carried on at seaside laboratories, rather than inland.

The most impelling lodestone to draw physiologists to the sea (just as in the case of the zoölogist or botanist) is, however, the physical and chemical nature of the salt water itself. The essential suitability of the latter as a home for protoplasm has often been emphasized of late, and justly; for though (as one contributor points out) we ought to regard sea water as a specific environment because salt lakes, very different in chemical composition, also support life, the sea (if judged by the variety of plant and animal forms that have developed there) is far the more suitable medium. And while this does not necessarily mean that it is inherent in living matter to be best fitted to exist in sea water or in some solution very similar to the latter, this certainly applies as a general rule, under conditions as they actually exist. Furthermore, it is the particular nature of the

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sea water alone that makes life, as we know it, possible anywhere in the sea outside a very narrow coastal strip. Were sea water not nearly as heavy as protoplasm (thus making flotation easy) and did it not carry in solution a variety of chemical compounds usable by plants as food, the abundant plant life of the seas could not exist at all except close to the lands: without plants there could be no animals except there, so that the whole oceanic basin would be a desert.

Sea water, furthermore, is not only a favorable, but a complete environment (for it contains in solution all the known elements not only in simple inorganic, but some also in organic combination), having properties that can be precisely defined, measured, and altered at will under controlled laboratory conditions, i.e., temperature, total salt content, concentrations of different solutes, ionic dissociations, osmotic pressure, and so forth.

Marine physiology therefore centers around sea water as an environment for life. And the most promising approach to all those interactions between protoplasm and its surroundings, by which life is sustained and which set all living matter apart from all non-living, is through quantitative study of the interchange between the cell and this environment. We need only refer to the very suggestive work that has been done of late on the selective permeability

of cell membranes and on the accumulation of ions. None of these interactions can be directly traced in the air, nor could be in fresh water unless the latter carried substances of some sort in solution.

But our present knowledge of the physical and chemical characteristics of sea water is so imperfect that we still lack the just physiological interpretation of what it really is, that is needed as the rational starting point in many lines of investigation. Before the physiologist can assay the rôles that organisms of various kinds play in the ocean equilibrium, and *vice versa*, he, or his chemical colleague, must measure, quantitatively, the periodic alterations of significant chemical constituents that take place in the sea water. Only now do we begin to understand the progressions of nutritive substances, and the regulation of their levels of concentration, as related on the one hand to depth, to distance from land, to seasonal periodicities, and so forth, and on the other, to organic production and destruction.

The question by what mechanism the cell is able to select out of the water those rare substances that, as it now seems, are of vital importance, opens the whole problem of the specific affinity of different cells for particular chemicals that forms the basis for all the structures that protoplasm manufactures. We might mention the secretion by diatoms of silica (an element relatively rare in sea water) in such

great quantity that at times they may almost exhaust the water of it; the ability of seaweeds to draw iodine and potassium from the surrounding water so much more efficiently than man can, that until other sources for these substances were discovered it was far more economical to obtain them from the ash of seaweeds than it would have been to concentrate them direct from the water by any method yet perfected or likely to be developed: the ability of certain unicellular animals (*Radiolaria*) to build their shells of strontia, a substance so rare in the water that only recently have analyses revealed its presence there. If any seaweed made equal use of gold, the commercial extraction of the latter from sea water (on the average there are about five milligrams gold per cubic meter of water) would not be the will-o'-the-wisp it has actually proved. A more familiar example of the ability of the living cell to select particular substances from the outside is the secretion of limy shells by a great variety of plants and animals, an ability responsible for vast deposits of calcareous sediments, of limestone rock, and of the modern coral reefs. The question of the draft made by different vegetable cells of specific solutes for their nourishment, as of nitrates and of phosphates by diatoms: or of the same solutes in different proportion, is now under investigation at many hands.

The degree of permeability of membranes for dif-

*Pulse Max ne
Boundary H₂O*

ferent solutions also holds the key to the riddle whether marine animals can feed directly on the organic substances in solution in the water, before these have been reduced to their constituent nitrates, carbonates, etc. The theory that they so do (the so-called 'Putter's theory') has been much discussed, but is still open.

Certain of the gross phenomena associated with such withdrawals of materials from the water of the sea by animals and plants are familiar enough; the formation of reefs for example, or local swarmings of diatoms. But little is yet known of the factors that control them. Why is it, for example, that organisms take out more lime in high temperatures and shoal water, more silica in low temperatures and in the deeps? The chemical reactions that have been proposed to account for such differences do not wholly explain them, and the vital mechanism back of this selectivity (perhaps the most fundamental of all the peculiarities of living substance) is still a mystery to us. Its solution (akin to the solution of life itself) may never be reached. But certainly its manifestations can be most directly studied in the sea, where, for example, we often find one group of unicellular plants thriving in water that some other group had already rendered barren for itself by denuding it of the chemicals on which it subsisted, and where the whole range of phenomena associated

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with the specific affinity of these lowly organisms for particular substances is effected on a vast scale by the simplest organisms.

All of this converges in turn upon the underlying problem of the basis for the group and specific differences in protoplasm: differences that are reflected in all the diversity of life that has existed on our planet.

Studies in this field have also a directly human interest, for through them there seems hope of learning how it is that our own body cells select one substance or another from our own food *via* the blood stream, a question about which we are still almost wholly in the dark.

As a final thought on a somewhat different plane, added to this report by one of its contributors, 'one of the present duties of physiology is the revivification and modernization of general natural history. Long experience with fragmentary investigations of the sea has at least made it clear that this association of interests is desirable, and that life in the sea is one of its most fruitful fields. Perhaps this is due to the fact that a certain mental humility often follows contact with the complexity and immensity of the ocean.'

3. MARINE BACTERIOLOGY

Present-day preoccupation with medical science makes us prone to think first of bacteriology in its re-

lation to human diseases. The problem of disease, however, seems not to be of great moment in the sea. Thus, while fishes (and no doubt other marine animals) do suffer from a variety of bacterial infections, and while the human aspects of bacteriology do reach into the sea to some extent, as when typhoid—and other disease-bacteria, coming from the land, gain foothold in the bodies of oysters, clams, or other shellfish, most of the pathogenic bacteria (though capable of living and multiplying in sea water with added nutrients) have been found to succumb rapidly in normal sea water. By and large, the disease-bacteria of man and of the higher animals do not thrive in the open ocean.

The problems of marine bacteriology that we wish to emphasize here are more akin to those of soil bacteriology, for they center around the rôles that bacteria play in keeping in motion the cycle of matter through its organic and inorganic stages in the sea. If we write less confidently on this subject than we have on oceanic zoölogy (page 127), or on marine physiology (page 152), it is because our knowledge of bacteria in the sea is still woefully scant. But such glimpses as have been gained of their activities there are enough to show that these must be assayed before we can hope to understand the maintenance of organic fertility in the oceans.

The simplest task of marine bacteriology is per-

haps to trace the direct service these lowly and minute organisms render to the larger in providing the latter with proteid food. That protozoans do feed on bacteria in the sea is established. In fact, recent studies suggest that in this passive way the bacteria that thrive on the organic débris accumulating in shoal waters, and the protozoa that prey upon these bacteria, are essential links in the food-chain of higher animals in coastal waters, where the echinoderms, mollusks, and others that feed on detritus gain their nourishment less from the latter direct than from bacteria and protozoa eaten at the same time.

This question is a quantitative one; the answer depends on the numerical distribution of bacteria regionally and with depth. In general, the sea water is known to be much richer in bacteria near shore, where land drainage maintains a state more fertile for them, than out in the open ocean; especially is this true of the forms that subsist on the excreta of animals. But viable bacteria have also been found to exist far out at sea, away from coasts, increasing in number down to a certain depth, while many of them at least are killed by strong sunlight. It is certain, too, that bacteria are abundant in many of the muds not only in moderate but even in considerable depths. Do these serve the whole category of mud-eaters as food on the slopes of the continents, and

should bacteria be regarded as the primordial meat supply of that belt of the ocean; or is their rôle in this respect important only locally? We know nothing of their relative abundance at great depths, or in the abyssal mud, except that there, too, bacteria do exist.

In attempting to interpret the food-cycle in the sea, bacteriologists must also take into account the possibility that among the bacteria devoured by protozoa and perhaps by the mud-feeders generally, there are enough of the sorts that can change carbon dioxide to organic carbon without sunlight, to form an important primary food for some animals, so short-circuiting the line from animal to plant and back again to animal, by freeing the latter from dependence upon the photosynthetic plants. The nitrifying bacteria discussed below fall in this autotrophic category, being able to obtain all their vital requirements from simple chemical compounds, such as ammonia, nitrous acid, and carbon dioxide. And there are other categories of bacteria similarly chemosynthetic; for example, the methane, hydrogen, and carbon monoxide groups. Beyond the fact that the nitrifiers and perhaps some of the others do exist in the sea, we have as yet no knowledge as to how important they are as sources of primary food-stuffs for animals. It is with regard to the inhabitants of the abyss where no ordinary plants can exist that this question is the most intriguing.

More generally significant than the simple relationship of bacteria to marine animals as prey for the latter, is their relationship to the circulation of nitrogen through its organic and inorganic phases in the sea. It has long been known that the sea water is nearly saturated with nitrogen gas at all times and places. But none of the ordinary marine plants, so far as we know (and certainly none of the marine animals) can use nitrogen in this elemental form, though every one of them requires nitrogenous nutriment. For the animals, this food comes in the long run from the plants; and all marine plants (except certain bacteria) are believed to depend for their existence on the presence of certain salts of nitrogen (chiefly nitrates) in solution in the sea water. The fact that the latter contains these salts reflects the activity of certain groups of bacteria, either *in situ*, or on land. These include the putrefactive bacteria, the nitrifiers, and the nitrogen fixers. Until the complex proteids and carbohydrates contained in the bodies of dead organisms are reduced to simple compounds they can be used only by carnivorous animals, by fungi and by bacteria; not by the photosynthetic plants.

Great amounts of nitrogen, it is true, in combinations directly usable by the latter, are contributed to the sea by discharges of river waters, carrying with them the drainage from the land, also from

air; but a greater potential source is the decomposition by bacteria of the carcasses of marine animals and plants within the sea. Bacteria of decay seem to be as ubiquitous in the sea as they are on the land; witness the rapidity with which carcasses rot in the water at moderately high temperatures. And not only can they usually be isolated from decaying fish, but certain of them are normal intestinal inhabitants of haddock, no doubt of other species of fish. As yet, however, we have no precise information as to how temperature, darkness, pressure, and the supply of available oxygen affect the activities of this putrefactive group in the deeps where much of this decomposition takes place. And this question looms large in oceanic economy because the rapidity with which carcasses break down (one of the two factors that in the end control the fertility of the sea) controls the state in which organic detritus reaches the sea floor in its descent from the upper layers, to maintain the reserve supply of dissolved nutrients, and so forth, in the deeper water.

Evidence at present available, especially the fact that mass production of diatoms reduces the supply of nitrates in the water, but not the supply of ammonia, indicates that marine plants as a group cannot utilize the end-product of putrefaction (ammonia) direct, but only after it has been transformed, by oxidation and combination with bases, into ni-

nitrates or nitrites. And so far as is known, this transformation proceeds only through the agency of certain groups of bacteria, the so-called 'nitrifiers.'

The chemical reactions that bacteria of this group bring about in sea water, under controlled conditions in the laboratory, are known. And their presence in bottom muds in various localities, both in high and in low latitudes, has been established by the fact that inoculation with such muds of salt water containing ammonia in solution results in the formation of nitrates. It has been proven by similar experiments that nitrifiers also exist in the water close to the bottom: likewise in surface water near land, but only in situations where there is much silt and detritus in suspension, suggesting that the bacteria in question are associated with the latter. But so far as I am aware, no direct evidence has been obtained that nitrifiers exist in the waters of the open sea away from the coast and from the bottom, though tests have been made to that end. Available experimental evidence therefore suggests that in the sea the alteration of ammonia into nitrates takes place on a significant scale only close to the shoreline and on the sea floor, not at all in the surface waters or in the mid-strata of the open sea. This, if correct, locates the chief zone of regeneration for nitrates by bacterial action as coinciding with the zone of regeneration for phosphates in shoal mar-

ginal seas, but as lying at a considerably greater depth in the ocean basins. But the correctness or reverse of this view remains to be established.

Our only present indication as to the scale on which the nitrifiers actually work in the sea is the rate and regularity with which the supply of nitrates and nitrites is regenerated in the surface waters, after it has been exhausted by abundant growths of planktonic plants. And to illustrate how small a basis for broad deduction is yet afforded by such data, I need only add that pertinent observations have so far been confined to short series of observations at a few localities in shoal water, and that owing to technical difficulties, few (if any) of the analyses for nitrates and nitrites that have yet been made have been entirely satisfactory.

We have still to learn whether we can interpret the responses of the nitrifiers (in rate of multiplication and efficiency of action) to variations in temperature, light, oxygen, and state of the ammonia and other organic derivatives present, by analogy with their activities on land: they may follow different laws in the sea. Definite information as to their relative importance in muds under deep and under shoal water is so far lacking. But these questions (about which different views are held, more on the basis of deduction than of observation) must be answered before we can assess the relative importance

of different depth zones of the sea bottom as sources for the regeneration of the salts of nitrogen. And this whole matter is especially pertinent at present, when the vital activities of planktonic plants are receiving so much scientific attention, because correct interpretation of the variations in abundance and in season of multiplication of the latter depends on a knowledge of the relative importance of nitrifying bacteria within the sea, of land wash, and of nitric acid from the air, as the agencies that maintain the stock of nitrates in the superficial stratum of water, or renew it there when temporarily exhausted. This applies particularly over the continental shelves, where planktonic plants reach their maximum abundance.

The possibility that the so-called 'nitrogen-fixers' may also add significant amounts of nitrogen salts to the sea water, in some regions, in forms directly usable by ordinary plants, must also be taken into account.

Bacteria of sorts that have long been known to assimilate atmospheric nitrogen in the soil, if they are also supplied with non-nitrogenous sources of energy, and to fix it in compounds usable by plants, have also been found widespread in the sea in shoal water, at localities as far apart as the Baltic, the North Sea, and the Indian Ocean: also in the plankton. Organic carbon going into solution in the

water from the breakdown of the bodies of defunct animals and plants supplies them with the chemical energy that they require to carry on nitrogen-fixation. There is experimental evidence that they are able to fix the nitrogen gas with which sea water is saturated, just as they do the atmospheric nitrogen in the soil on land. And so far as it goes, any conversion that they effect of nitrogen gas to nitrates in the water must be of direct importance in marine economy, by making a nitrogen supply available for marine plants which cannot use it in the gaseous state. But we have yet to learn how to assay, in quantitative terms, the frequency with which such bacteria have been found associated with seaweeds in shoal waters (where the concentrations of life are the greatest); neither have we any direct information as to whether they ever operate on a significant scale there, or in any other part of the sea. In fact, there is no general agreement, yet, as to the quantitative importance on land of such of the nitrogen-fixers as live free in the soil; and it is to this group that the marine nitrogen-fixers belong that have so far been found in the sea. Neither is it known whether there is anything in the sea comparable to the symbiosis that exists on land between other nitrogen-fixers and certain leguminous plants. Final solution of the general problem of whether the nitrogen-fixation by bacteria in the ocean is anything more than a

minor event would be one of the welcome gifts that marine bacteriologists could offer to oceanic biology.

Before any sound explanation of the nitrate and nitrite cycle in the sea can be arrived at, the activities of the denitrifiers there must also be worked out quantitatively and empirically as well as qualitatively and by deduction, for these (as far as they operate at all in the sea) tend to denude the water of nitrates by breaking these compounds down to ammonia, or even to nitrogen and its oxides, thus putting them out of reach for the photosynthetic plants.

It has long been known that denitrifiers do exist in the sea water, and much discussion has centered around their supposed activities there. But, lacking quantitative information, we have no clear conception of the scale on which they actually effect such losses in the open ocean, both because of our ignorance of their abundance in its different parts, and (more important) because the factors that govern their denitrifying activities in the sea water are not yet understood. It has long, and generally, been believed that bacteria of this group operate more efficiently at high temperatures than at low. Arguing from this supposed fact it has often been suggested that the scarcity of nitrates actually recorded in the tropics, as contrasted to colder waters, reflects greater activity of these bacteria in warm seas; consequently, that the regional differences in the losses

of nitrogen that they cause are responsible for the supposed general paucity of phytoplankton in the tropics as compared with higher latitudes.

But this theory, like many another that has been set up in oceanic biology, is based on only one factor in the environment, when actually others may be more important; and on a numerical abundance of the organisms concerned which, while easily maintained in the laboratory, may never exist in the open sea. Recent experiments, for example, have suggested that while temperature controls the rate of activity of the denitrifiers, they actually attack nitrates only when oxygen is deficient. This would point to great possible losses of available nitrogen, by their activities, in the bottoms of certain enclosed basins, in the mud generally, and wherever oxygen is relatively scarce in the mid-strata of the oceans, but to little or no denitrifying activity on their part in the surface layers which are nearly saturated with oxygen. If, however, these bacteria are active in the mid-depths, the results of their cumulative work there may lead to a great loss of nitrogen that must be made up in some other way, because much of the decomposition of dead carcasses, sifting down from above, takes place at this level. What is needed here is empiric determination of what actually does take place, more than theoretic discussion of what might happen.

How active the denitrifiers are in the mud is also a live question, because the sediments on the sea floor, in deep water as well as in shoal, contain considerable quantities of organic nitrogenous compounds, which, so long as they continue in chemical combinations subject to the action of putrefactive and nitrifying bacteria, are a potential food supply that may be brought to the plants in the upper waters by vertical currents. In the Gulf of Maine, for instance, the bottom muds contain on an average about as much nitrogen as good garden soil, much of which is probably distributed throughout the water at the seasons when vertical circulation is most active. It may be assumed that a scarcity of oxygen everywhere in the mud below the superficial skim sets the stage for the destructive effect of the denitrifiers there, unless the temperature be too low for them. But we are still entirely in the dark as to how effectively they do act in the mud, i.e., what rôle they play in preventing the accumulation of nitrates in the submarine deposits, for while these salts are extremely soluble in the sea water, organic particles tend to be trapped in the mud wherever sedimentation is rapid, and thereby to be protected from the action of the water. Any nitrogen locked up in this way would be a dead loss to the oceanic complex until in some way brought back again into circulation.

It is because animal life in the modern ocean

depends vitally on the presence of photosynthetic plants for its ultimate food supply that we have so far stressed the general problems that center around the rôles of bacteria in keeping the sea water fertile for these plants by maintaining the stock of dissolved nitrates and nitrites, or by replenishing the water with these substances when active multiplications of diatoms, and so forth, have locally reduced the supply below the minimum concentration necessary for the nourishment of marine plants.

We have yet to learn whether bacteria of fermentation, or any other fermenting organisms such as yeasts, are abundant enough in the open sea or in the sea bottom (if they exist there at all) to play any broad scale part there in the cycle of carbon, as bacteria certainly do in the cycle of nitrogen. Whether the carbohydrates contained in the carcases of animals and plants are devoured by scavengers, or whether they simply disintegrate in the water to their ultimate breakdown, their end states are carbon dioxide and water. In the second case it is possible that fermenting bacteria, and so forth, play a significant part in the process. But lacking direct experimental evidence it must not be assumed that this is necessarily so, because it is also possible that enzymes formed within the bodies of animals and plants in life in their normal metabolism are the agents principally responsible for

the breakdown of their organic carbon-compounds, after death has destroyed their immunity to self-digestion.

We also need to know what part bacteria play in breaking down the more refractory organic substances that would accumulate on the bottom of the sea if there were not some mechanism to disintegrate them and to bring them into solution in the water. Specifically, what quantitative rôle do bacteria play in the sea, in the destruction of the agar from the stalks and fronds of seaweeds that is constantly taking place under water — a substance resistant to most bacteria? Bacteria of the sorts that do attack agar have recently been found in brackish and in salt water. But, so far, it has been only in the tropics that their presence in such situations has been established, whereas it is in higher latitudes (and lower temperatures) that the great concentrations of ordinary seaweeds exist, and the great overturn of agar and of similar hemicelluloses takes place. Thus it still remains an open question how far the annual disintegration of the millions of tons of kelp, and so forth, results from bacterial activity, or how far it simply reflects the solvent action of the sea water itself. We face this same problem with regard to the destruction of the chitin in the shells of dead crabs, shrimps, and other crustaceans, and of the oil from diatoms and copepods.

Bacteria certainly play other important rôles, which, as yet, we only glimpse, in the chemical changes following the alteration and decomposition of organic matter that takes place in the deepest water and in the bottom sediments. Here we think at once of the forms that reduce sulphates in the absence of oxygen to sulphides in the black muds of shoal waters, especially in enclosed basins with little circulation. Bacteria, too, are indirectly responsible for the accumulation of sulphurated hydrogen in the deeps of the Black Sea and of certain fjords. We greatly desire more detailed bacterio-chemical studies of the deep water of other such basins, e.g., of the Sulu Sea. The activity of these same groups needs to be studied in the open ocean, where, because of the active circulation of the water, their effects are not so apparent. We know almost nothing about the activities of bacteria in the abyssal muds; a question especially important in connection with the deposition of iron, and from other points of view, as well.

It is still a live problem whether, or to what degree (if at all) bacteria cause calcium precipitation in the sea. This question (as is usually the case) cannot be answered simply by finding out (as has been done) that certain of them can precipitate lime out of sea water under special conditions in the laboratory; we must also learn whether they are associated with the mass precipitations in the sea in significant numbers;

also whether there is sufficient supply of nutrients in these situations to support their growth, and (by studies of physico-chemical relationships in the water) what chemical changes such precipitation involves. The necessity for uniting several disciplines in this case illustrates how broad a view must be taken of biophysical and biochemical problems as a whole in the ocean.

A few more problems that have a general bearing both on bacteriology *per se* and on the science of the ocean, may be mentioned. What rôle is played, for instance, by the luminous bacteria, whether as saprophytes or as normally symbiotic with animals and plants? Do these bacteria exist at abyssal depths? If so, are they sufficiently abundant for their luminescence to be important in the vital economy of deep-sea animals? Do they, perhaps, help to make vision possible for the large-eyed benthonic fishes of the abyss, most of which are non-luminous themselves?

The marine anærobes have received scant attention. Here the recent discovery that CO₂ tension rather than oxygen tension is the requirement that distinguishes them from aerobes, emphasizes the necessity for further information as to chemical conditions in the water.

A bacteriophage has also been reported in the sea by French oceanographers. How generally this

principle (destructive to bacteria) is distributed through the oceans, and how effectively, if at all, it combats the manifold activities of marine bacteria remains to be learned.

Microörganisms other than bacteria have also been found in the ocean and may have a quantitative importance in the chemical processes that have been enumerated comparable to that of the bacteria proper, a relationship that has been well established in the case of soil microbiology. The Actinomyces may be cited as a group that are worthy of attention as are the bacteria themselves: this also applies to the yeasts.

The answers to the principal questions that the oceanographer may properly ask of the bacteriologist are not as directly available as mere enumeration of them might suggest; in this particular field, perhaps more than in any other division of sea science at present, it seems certain that no great headway can be made until technique is perfected. No one instrument will solve the problem of bacteriological sampling in the sea. For purposes of enumeration the sample must be large: to concentrate it prior to microscopic enumeration is often difficult. The sampling of water for culture work, when small volumes suffice, presents few obstacles, but it is otherwise with the sampling of mud, for in this case it is necessary to recover an undisturbed specimen so

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that the sample can be examined serially, commencing for example with the top millimeter, unmixed with lower layers and unwashed by superposed water on the ascent. We have also to learn what modifications of the routine media, or of those favorable for soil organisms, will give the maximum counts of bacteria from a given sample of ocean water. We shall not be able to assay the significance that should be attached to the physiological activity of marine bacteria until we are able to grow most of the organisms that can be found in the water. And, in general, we must emphasize that random procedure, and approximate technique can never serve as the basis for evaluating the general share of bacteria in the economy of the sea.