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Environment

What kind of biological research would ultimately make the greatest contribution to achieving full utilization of the sea food resources? When I put this question to a number of leading marine biologists and oceanographers of America and Europe, they were remarkably unvarying in their advice: Study environments, seeking to learn how chemical, physical, and biological characteristics of sea water influence its fertility and thereby control the abundance and distribution of organisms. The many elements of environment that combine in various ways to make up qualities of fertility are much less localized in the sea than on land, for they are in constant movement horizontally and vertically. They are carried by currents and are therefore far-reaching in their influence. An event happening in one part of an ocean can eventually, perhaps months later, affect production of living things hundreds of miles away. Every species has its own peculiar set of environmental conditions for optimal production; what is essential to one species may be inimical to another. Thus the production of environments in the sea is an elusive subject to study. What is it? What are problems of understanding it that need to be solved? What is present opinion about the geographic distribution of the more productive areas? What are the important gaps in research programs concerning environments? These are questions which this chapter discusses.

There has been much speculative talk about exploring the depths of the sea to find new species of organisms that could yield large harvests, of diking off salt-water marshes and sloughs and cultivating

them for fish farming, and of growing plankton artificially or at least harvesting it in the open sea. Such concepts as these underlie dreams of feeding the world from the sea. What kind of research would be required to accomplish these objectives? What processes would be required to demonstrate their economic feasibility?

Here, as in all scientific pursuits, we must seek principles first, for all of these dramatic measures involve using environments intelligently, somewhat as agriculturists do. That is to say, they involve locating and working the most fertile areas, harvesting selectively to produce the most profitable balance of populations, controlling rates of harvesting, reducing predators, and, in some places and under some circumstances, farming environments by cultivating and fertilizing and by planting stocks which are especially adaptable to local conditions. How successfully we might do any of these things would depend on how intimately and thoroughly we knew the principles by which the intricate mechanisms of environment cooperate to support the lives of useful species. This implies the necessity of studying environments.

Throughout this book I use the phrase "an environment" in an unorthodox way to denote a habitat together with its resident communities of plants and animals. This will avoid some uses of words that fit better in a textbook on ecology.

The environment of a species is its cosmos, the milieu in which it lives. It includes its physical setting—the sea water, with all its mineral salts and dissolved organic chemicals, regimes of temperature and of solar radiation, and structure and composition of the bottom. It includes the whole assemblage of different species of plants and animals that live together and affect each other beneficially or harmfully. It is a system of systems, with inorganic and organic components.

An environment (as I am using the term) is an ecological unit, that is to say, a part of the sea which has peculiar properties that satisfy the physiological requirements of a population or a number of species of populations which live together there. Examples of environments are a deep-flowing water mass, a current at the surface, an area on a bank where the ground is muddy, or an area where it is gravelly. A gently sloping sandy open beach, an estuary, a brackish marsh—all are types of environments. Their boundaries and other characteristics can be extremely plastic, with dimensions, position, and physicochemical properties pulsating continually in response to meteorological and other external influences. The populations which they contain pulsate with them. These changes usually follow a more or less seasonal pattern, superimposed on

very long waves with durations of years or even decades, the whole complex pattern marked by brief, sharp fluctuations.

Environments rarely have sharp boundaries, and they are never independent entities, but affect each other in many ways. Events happening in one environment may have consequences in an entirely different one many miles away. Thus it is often difficult, and beyond a certain point, unrewarding, to try to isolate one environment for study without reference to those others that influence it. Few species confine themselves to one type of environment throughout life, but change in response to changing physiological demands. Oysters, for example, which are free-swimming during infancy, settle down to become fixed early in life, and remain so until death. Prawns spend their youth in sloughs and salt-water marshes and later move to sea, eventually traveling rather long distances offshore to spawn. Flounders, like many other kinds of groundfishes, are pelagic during egg and larval stages, during which period they are carried far by currents. After metamorphosis, they settle to the bottom, where they remain thereafter. But even then they are not quite sedentary, for they tend to migrate toward shore in summer and away from shore in winter; and as they get older, they move into progressively deeper water. Herring, on the other hand, are stuck to the bottom during their egg stage, but after hatching, the larvae drift with the currents. After metamorphosis they live very close to shore in bays. As they grow older they seasonally move offshore into deeper water. In inhabiting a succession of environments from birth to death, broods of a species become, in effect, successions of populations, each differing from the others, yet all connected by the strong thread of life history. Events during a brood's sojourn in any one of its environments can prove fateful to the remainder of the life of a brood. Consequently, a proper study of the biology of a species, such as an important food fish, must include the whole gamut of its environments in order to understand the principles controlling its vagaries of occurrence and abundance.

There is a great amount of information about marine environments of the world. Some of it is well organized and easily available in published literature. Much of it is scattered, buried in files, uncollated. Some of it is only in people's heads. What there is originates from various sources. To begin with, fishermen, from the most advanced to the most primitive, living on the sea and depending on its resources as they do, have learned a great deal about what is associated with the occurrence and nonoccurrence of the species that concern them. Quite a few published works are little more than systematized compendia of information gleaned from fishermen.

Valuable though fishermen's knowledge is, however, it often includes a great deal of superstitious lore.

Conclusions from scientific research are more objective, less influenced by tradition, and therefore more dependable than those from fishermen's observations. A large body of systematized knowledge about sea environments has come from expeditions which museums and institutions of marine research have sent out all over the world to take samples of various kinds in various regions. These have collected and described specimens of animals and plants, estimated the abundance of the fauna and flora, and sometimes the rates of its production. They have sampled the water at various depths, analyzed its chemistry, recorded the temperatures, and determined the direction and rates of flow of currents. They have charted the topography, examined the geology of the bottom, and done many other things of scientific interest. The thoroughness of all this work varies geographically, for expeditions have visited some regions much more frequently than others.

The most comprehensive knowledge of environments relates to a few relatively small areas where great fisheries are carried on. This knowledge results from constant systematic study by institutions of marine biology and hydrography which are conveniently located. It is such laboratories which make contributions that have been most valuable to the intelligent use of marine environments. Figure 8 (page 28) shows that these most intensively studied areas of the marine world are in fishing grounds of the North Atlantic Ocean, principally the North Sea, the Baltic, including the Gulf of Bothnia, and the Norwegian Sea; the New England Banks; a segment on the coast of southwestern Africa; the Scotia Sea in the Southern Ocean; the east coast of Australia; the Red Sea; the west coast of North America, principally California and northern Baja California, Puget Sound, and British Columbia; and the northwestern part of the North Pacific in the vicinity of Japan, including the Sea of Japan. Among the least studied areas are the entire Indian Ocean, particularly the Arabian Sea and the Bay of Bengal; the Indonesian Sea; the Arafura Sea; the Coral Sea; and large areas of mid-ocean in the Pacific.

Scientific knowledge about the oceans and their resources is unevenly distributed; so also are marine research facilities. There are about 240 laboratories in the world for studies in marine biology, fisheries, and physical oceanography. Close to 90 per cent of these are in the northern hemisphere; 85 per cent of them are north of 20° N. latitude. In the tropics and the southern hemisphere there are long stretches of coast without benefit of any marine laboratories.

Thus serious gaps in knowledge of marine environments are geographic, and they are associated with a lack of research facilities in the areas about which ignorance is greatest.

In northern regions, the existence of established fisheries had much to do with stimulating the founding of marine laboratories and determining their location. In the tropical and southern regions it is the other way around. There it is proposed to establish marine laboratories to stimulate the founding of fisheries. They should be located as close as possible to production areas. This is an important point, because the sea is not evenly productive. Indeed, much of it is not rich enough to support fisheries at all. Figure 14 (page 37) shows regions where oceanographic conditions are conducive to heavy production of organic matter and therefore, presumably, of fishery stocks. Even though these areas are restricted, they still are very large. Most of them are unexploited or far underexploited. They have been studied very little, and there are few if any facilities for studying them. This is more or less true, for example, of the Benguela Current off southwestern Africa, the north and south equatorial currents of the Atlantic, the northeast coast of South America, the western shores of the Arabian Sea, the Peru Current, and most of the Southern Ocean. Any of these regions would be a profitable area of study for a laboratory.

It is in the long-established institutions of Europe and North America that the classical research techniques of general marine biology, fishery biology, and hydrography have evolved. In general, these laboratories are approaching the advanced and extremely difficult stage in their studies where they must determine how the various elements of environment which they have minutely examined fit together to compose an integrated mechanism—the environment-as-a-whole. It has been taking a long time to reach that point. The road is long and tortuous. There have been many false starts and blind diversions.

A new laboratory can profit by the mistakes which the older ones have made as well as by the principles which they have discovered. Nevertheless it too must go through a long initial stage of exploration and analysis before it can have assembled enough material for synthesis. Even under the most favorable conditions it could not spring into being full-blown. It would be better to begin on a modest scale. From there it would succeed provided it were well backed financially from the start, and provided the people who controlled its existence had the will for it to grow and a sound plan for its future.

The initial program may concentrate on taking a comprehensive inventory of what there is in the region. What are the species of animals and plants? How are they distributed? What are the seasons of their occurrence? As this knowledge grows, the studies should become more quantitative—how much is there? At the same time there need to be built up taxonomic reference collections, a library of world literature on marine biology, physical oceanography, and fisheries, bibliographies of published scientific literature about the region, and all available pertinent unpublished information. As soon as possible, a hydrographic program should begin to determine the characteristics of the water, the pattern of currents, and their connections with the distribution and numbers of animals and plants. Fisheries studies should accompany this developing program, guiding it, fitting into it, taking every advantage of its results, and covering the life histories and behavior patterns of the commercially interesting species.

Gaps in the programs of well-established institutions are not immediately obvious, but nevertheless there are gaps. The principal one is in the interpretation and integration of data relating to all the diverse elements of environment. The center of interest in most marine laboratories is the science either of biology or of geophysics. Marine biologists tend to focus attention on species of animals, physical oceanographers on the chemistry and movements of water. Thus they divide into two groups, each studying a different aspect of environment. What is most seriously needed here is some means of combining these two points of focus to produce a single, full-dimensional picture of the whole environment. This might be best accomplished initially by adding special teams to these institutions. The members would have among them a variety of talents and specialties; nevertheless the subject of their research should always be environment. One of their principal functions would be to assemble all available facts about the various elements of environment to study how they fit together—facts about climate, weather, currents, comparative physiology, life histories, faunal composition, fish catches, sizes of populations, and so forth. In addition, they should engage in laboratory and field studies on such questions as these:

What do animals and plants demand of environment? What are the elements of environment? What are the mechanisms of their actions? What are the boundaries of environment of the various species? Here is needed a tremendous fund of knowledge about the life history and physiology of the many organisms that are part of

the more important environments. In the most studied parts of the oceans, such as the Gulf of Maine, research to develop such knowledge has been done for less than 15 per cent of the total species. In other places of interest, such as the coasts of South America and Africa, it has hardly been done at all. The most obvious questions to study about each species are these: Where, when, how frequently and under what circumstances do the individuals reproduce? How fast do they grow? How long do they live? What are their competitors and enemies? What do they eat? How do they behave in response to various stimuli? What are their routes of migration or transport? How are they affected by the submarine weather and climate? How are they affected by such chemical constituents of the water as trace elements and organic substances? What are the forces inducing their oscillations in numbers? What rhythms are in their oscillations? As information on these questions accumulates, it should bring out how the species of any given environment fit together. On that point, which is particularly important in practical fishery problems, our present knowledge is almost nil. How does one species relate to another as predator, competitor, or fodder?

Embodied in these questions is the problem that troubles people in the fishing industries more than any other. What causes fish stocks to fluctuate in abundance and availability? For the last twenty years or so, fishery biologists have centered their researches on the dynamics of fishery populations. Accordingly, they are engaged in acquiring the numerical data for formulas designed to determine the yields to be expected from various levels of fishing effort. One of the most important elements in these formulas is always *M*. *M* is a measure of the sum of the fatally adverse effects of environment upon a population. It stands for rate of natural mortality, that is, mortality from causes other than fishing. It is exceedingly difficult and expensive to measure this *M;* indeed no method of measuring it continuously has yet been devised. For that reason, and also because it is presumed that over periods of several years it fluctuates about a level, the natural mortality rate is treated as a constant. Nevertheless there is evidence to show that the range of its fluctuations can be very great.

There is no universal natural mortality rate in the sea. It differs between species. Within any one species it differs between populations and within a population it differs between localities. It changes throughout life, being highest during infancy and decreasing with age. It fluctuates from year to year. For several years it may be almost negligibly low, but can suddenly assume disastrous proportions. A stock can be reduced almost to the vanishing point

by an abnormally long period of unfavorable weather, by an epidemic, or by a rise in the abundance of a species which is a competitor or a mortal enemy.

Marine animals that are not permanently attached, like herring, move in and out of the range of fishing, usually, but not always, with a fairly regular seasonal pattern. Sometimes whole populations or only parts of populations fail to appear on the usual fishing grounds and remain absent for weeks or even for years. Their sporadic and transient reappearances suggest that they have moved to other parts of the sea for a while; in other words, they have become unavailable to fishermen operating on the old fishing grounds. It is sometimes difficult to distinguish such migrations from mortality of the population.

Each of the many biological and physical elements that contribute to mortality in a population fluctuates in one way or another, and its relative importance in the environment of a species may also fluctuate. Consequently, the faunal composition of any environment fluctuates. The more we can understand the mechanisms of these changes, the more accurately we will be able to explain and predict fluctuations in fishery stocks. What is the nature of those mechanisms? To throw light on that baffling question would be one of the most useful achievements of an environmental research team.

What is the causation of variations in abundance, availability, and quality of marine organisms? The practical consequence of these variations is that fishing is a terribly hazardous investment. This is true in varying degrees everywhere, regardless of the fishery, whether it be for fin-fish or for shellfish, in northern seas or tropics. To begin with, the year broods of all species vary in size. That is probably a safe generalization. An extremely good cod brood, for example, may be as much as fifty times greater in numbers than an extremely poor one. A fluctuation may affect all the stocks of a species over a very large area, or only those in a particular locality.

Since the earliest days of marine research, biologists have sought to discover causes of fluctuations by watching for correlations between the size of year broods and those physical attributes of the environment which they know how to measure—temperature, concentrations of inorganic nutrient salts, and speed and direction of currents. To this day, however, no one has found a perfectly consistent correlation that has gone beyond a few seasons. The breakdown of a correlation does not necessarily mean that it was a spurious effect while it lasted, but that elements dominating the mechanisms of survival have given way to others, as they may do sporadically. Not only do year broods fluctuate; virtually whole

populations of the adults of some species may disappear from the range of fishermen's activities. This may be the result of mass mortalities, shifts in environment, or overfishing. It is often difficult, with such meager information as is usually available, to be certain which of the three it is. In any event, a species that has thus disappeared sometimes remains absent for ten or twenty years, then reappears in numbers as great as ever. This sort of thing happens with species that are not exploited as well as with those that are. For example, in recent years squat lobsters (*Munida* and *Galathea*) have disappeared from the area about Plymouth, England, where they had previously been abundant. Similarly, sea urchins have become greatly reduced about Cape Cod, Massachusetts. Bluefish are again abundant on the Atlantic coast of North America, where they had been scarce for almost twenty years.

The biochemical composition of marine organisms goes through seasonal cycles which are probably related to the reproductive cycle, but it also varies geographically and undergoes fluctuations from year to year that must be related to something in the environment—perhaps its fertility. For example, in a given locality the menhaden, a herring-like fish used for fish meal manufacture in the United States, may yield no oil in some years, and in others as much as 60 gallons per ton. In a single month of one year it may vary between 5 gallons per ton in one part of its range, and 40 in another. The chemical composition of the marine algae—minerals, vitamins, carbohydrates, and proteins—fluctuates remarkably, and so far, inexplicably (see pp. 276–79). The mechanisms of all such fluctuations are involved with the mechanisms of environment.

Among the organisms inhabiting the sea are pathogenic (disease-causing) bacteria, rickettsiae, protozoa, fungi, and viruses. At times any of these can rise to epidemic proportions and have devastating effects on susceptible populations. Since this subject is discussed in a separate chapter, it is enough to say here that the study of the place of disease in marine ecology has been almost completely ignored in research programs. What elements of environment govern fluctuations in the occurrence of disease? What are the effects of diseases on animal numbers? These are questions with which an environmental research team would be deeply concerned.

A complex of problems centers around the basic fertility of the sea, which is an attribute of environment that bears most significantly on fishery stocks. In studying this topic, it is necessary to draw heavily on the work of fishery biologists on the one hand and of physical oceanographers on the other, and here a team of environmental scientists could serve as a cementing agent to draw the two

groups together in planning their respective programs and in interpreting their results. In the following pages, I shall discuss fertility of environments to suggest the scope of a research program in this subject.

Animals of the sea, like those on land, can prosper only in fertile environments; and just as on land, fertility is measured by the assemblage of physical and chemical properties that make it possible for plants to grow. The great bulk of sea plants is in the form of phytoplankton. Although phytoplankton occurs in the surface layers all over the oceans, the rates of its production and the quantities produced vary widely from one situation to another. They also run through seasonal cycles and fluctuate from one year to another. Fertility, through its relation to the production of phytoplankton, is the foundation on which the abundance of all marine resources is based. It is therefore a subject of the greatest pertinence to scientific sea harvesting.

Only plants, through the process of photosynthesis, can transform inorganic chemicals into organic food. Animals cannot do that; they can live only by eating, and they can eat only as much as is produced in their environment or is carried into it by currents. Some species eat mostly phytoplankton; others subsist wholly or in part on other animals; still others are omnivorous. But whatever their food habits, the rate of production of animals in the sea is set by the rate of production of plants. Sedentary animals depend on the food pyramid supported by the plants which occur in the area where they reside. If these animals happen to be carried to an unproductive place during their drifting phase, they starve. Roaming animals, on the other hand, such as swordfish or squid, which have broad environmental tolerances, go searching for areas where food is sufficiently plentiful to satisfy their rapacious needs. When hunting becomes unrewarding in one place, they can go to another. Even though they feed high in the food pyramid, they nevertheless depend on a rich production of phytoplankton to support the food in the various centers which they visit.

The most immediate effect of phytoplankton is on the herbivorous animals, that is, chiefly small invertebrates and very young postlarval fishes. Here there is a reciprocal relation, for the rate at which herbivores crop the phytoplankton influences the rate of its production, and that in turn influences the rates of production, growth, and survival of the grazing herbivores. Among carnivores, the same kind of relation holds between populations of predators and of their prey. Such relations obtain among all the populations living in an environment; they depend on the rates of metabolism,

reproduction, and growth of each population. These rates vary widely from one species to another. Within any one species, they vary with temperature and other characteristics of the environment. Obviously, the causes of oscillations in populations are exceedingly complex and therefore exceedingly difficult to trace. However, the fundamental, all-pervading influence is fertility; for the basic food, that is, the plants of the phytoplankton, like those of land, cannot flourish without material with which to synthesize their food.

Phytoplankton can utilize light only in the uppermost 30 to 300 feet of water. That being where they live, that is where they must obtain all their required nutrients. However, the sources of natural refertilization, that is, the waste products of the living plants and animals and the decomposing bodies of the dead, sink continually to levels deeper than the zone which the light required for photosynthesis penetrates. In high latitudes life flourishes in the sea from spring into fall, the phytoplankton and the zooplankton going through alternating cycles, the animals reducing the plants by grazing, and all diminishing to low ebb by late fall. Growth can resume only after the fertility of the surface environment is restored. This is accomplished through seasonal climatic and hydrographic mechanisms which bring about exchange between the nutrient-rich deeper waters and the impoverished surface.

This exchange occurs where cooling in the winter causes the surface water to become denser and heavier than that at lower levels. As this relatively heavy water sinks, it is replaced from below by rising lighter water, which is rich in nutrients. In the spring, in high latitudes, when the amount of daylight increases, the phytoplankton resumes its cycle of production.

Elsewhere, chiefly in lower latitudes, there is another mechanism which brings enriched water to the surface. In certain places, long persistent seasonal winds blow from one direction. For example, northwest winds prevail along the California coast from early spring to midsummer. The water which these winds push is deflected sharply by the action of the earth's rotation (to the right in the northern hemisphere, to the left in the southern) and is replaced by "upwelling" from below. Upwelling is a prominent feature of the hydrography along certain coasts (California, western South America, western Africa). Wherever it occurs it is associated with heavy production of organisms and rich fishery resources. A similar result occurs in the open sea wherever divergences exist. These are zones where the surface currents separate under the combined influences of wind, the earth's rotation, and density differences. To make up for this loss, water rises from the depths. Unlike upwelling or

winter overturn, this process may operate the year round, as along the equator in the Pacific.

A meeting of currents from different directions may also result in mixing and local divergences, with rising of deep water, resulting enrichment of the surface, and high productivity. This happens off the northern islands of Japan, where the warm, northward-flowing Kuroshio meets the cold, southward-flowing Oyashio; it happens south of the Grand Banks of Newfoundland, where the Gulf Stream meets the Labrador current. These areas, and others where similar situations obtain, are extremely productive fishery grounds (see Figure 1, page 15).

Exchange between very widely separated places occurs by simple horizontal movement of water. Perhaps the most extreme example of this is the great transport of surface water at a rate of something like 6 million cubic meters a second from the Antarctic up to the far reaches of the North Atlantic. This great mass of water comes from various sources—some of it from the southern hemisphere, some from the Mediterranean, some from around Greenland—all of it water that had become depleted at the surface, had sunk, and flowed southward at deep levels. All along the way it had become replenished with nutrients from the decay of sinking dead organisms. Around the antarctic continent it rises rich in fertilizing substances, to nourish one of the most productive areas of all the oceans; thence it returns ultimately to northerly seas.

Thus it is the vertical movement brought about by such processes as upwelling in some parts of the world and winter cooling in others that brings inorganic nutrients and perhaps also biologically important organic substances from deeper water to the surface where they become available for the growth of phytoplankton. The intensity of these processes varies seasonally and annually, and this has much to do with variations in the production of plants and animals. And it is by the horizontal movement of water, which also varies continually in speed and direction, that all the properties of environment—nutrients, temperature, plankton—are transported, sometimes to places far removed from their regions of origin. John Tait, of the Scottish Home Department, has written the following on this subject:

Currents control the distribution of temperature and other physical and chemical properties of the sea. They control the distribution of the ultimate food organisms on which all marine life depends. They control further the dispersal of fish eggs and of the youngest fishes until these acquire motive power of their own, and, in the reproductive stage of a fish's life, which, as it were, completes a cycle, they govern very largely, if not entirely, the movement of fishes

towards the places where those physical conditions exist in which alone reproduction will take place.[1]

An example of the influence which movement of water can have on a fish population is the case of the Pacific sardine. Between 1947 and 1953 this species disappeared from the coast of California. During the preceding thirty years the sardine fishery had gradually grown from its inception into the largest of all American fisheries, producing more than 500,000 tons annually. The supply failed first in 1947 in the northern part of what people had assumed was the normal range of the species. For a while it looked as though this might be a local fluctuation and perhaps the fishery would hold up as well as ever off southern California. However, it failed there too, at length, so that by 1954 fishermen caught less than 70,000 tons. Apparently this dramatic disappearance of a great fishery resource is largely the consequence of a change, the nature of which is still unknown, in the regime of hydrographic conditions on the Pacific coast of North America.

The principal elements in this pattern are the California Current, which flows southward, an inshore complex water mass of variable characteristics, which includes a northward-flowing countercurrent, and the northwest winds that prevail along the coast during spring and early summer. At this season, as a result of the action of these winds and of the earth's rotation, surface water turns seaward while deeper water wells up to replace it. This upwelled water carries phosphates and other nutrients that had sunk and accumulated during the preceding winter and fall. Scientists studying sardine problems have described these processes thus:

> Between the California Current and the coast, the region in which sardine spawns and is fished, appear complex systems of countercurrents and eddies, changing with the changing seasons. Winter ordinarily finds a strong, narrow countercurrent flowing northward along the entire coast. When the countercurrent is absent at the surface, as it usually is during the summer, oceanic eddies, great lazily revolving masses of ocean water, form in the inshore region. Such eddies usually form near Central California, near the Channel Islands of Southern California, and near Punta San Eugenio in central Baja California.
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> The most persistent of the eddies is located near the Channel Islands. This giant wheel of water, some 100 miles or more across, rotates slowly counterclockwise. Its center is characterized by the "enriched" water that has ascended to the surface from a depth of 700 to 800 feet ("upwelling"). . . .[2]

These seasonal shifts may be closely associated with changes in the subsurface countercurrent.[3] This current contributes somewhat to upwelled water, at least in the deeper layers. As a consequence of meteorological variations, it fluctuates in intensity and in the

distance which it travels at the surface. A strong development of this current seems to be associated with northward incursions of sardines and of their spawning grounds, with large year broods and with good fishing. This may result from the countercurrent transporting the environment optimal for the well-being of sardines, which includes temperature and other physical characteristics of environment as well as food.

The United States Fish and Wildlife Service's Pacific Oceanic Fishery Investigations, under the leadership of Oscar Sette, have demonstrated that divergence and upwelling at the equator enrich the surface waters with inorganic nutrient salts which stimulate the production of plankton. These plankton-rich waters drift northerly to a convergent zone. Experimental longline tuna fishing has consistently proved to be more successful there than in areas adjacent to this system. On this, Sette writes:

> The quantities of catch and the positions of the zone in the north-south direction have varied considerably, probably in response to accelerations and decelerations as well as the swaying north and south of the current system. Although our observations have not had sufficient continuity in time and space to elucidate these variations, it remains quite clear that the divergence-convergence features of the transverse equatorial circulation provide the basic support for a persistent concentrated stock of yellowfin tuna.[4] [Figure 14, page 37.]

Alfred Redfield,[5] of the Woods Hole Oceanographic Institution, has shown how the circulation of water affects the distribution of zooplankton in the Gulf of Maine. The dominant feature in the circulation of this body of water is a great anticlockwise eddy, which in the surface layers flows at an average rate of about seven miles a day. The eddy is fed by water which comes in on its eastern side from over the Nova Scotian Banks; and it loses a corresponding amount which escapes southward and eastward across the end of Georges Bank. This inflow and outflow varies seasonally and from year to year. It is at its peak in winter. The new water that comes in at that time is relatively barren, and remains so until spring, when conditions become favorable for growth and reproduction. The water of the eddy is by no means completely replaced at once, however. Much of it remains in the southern part of the eddy supporting a rich population of plankton that had grown up the previous summer and had become only moderately diminished by the adverse conditions of winter. In the spring and summer, when the inflow and outflow decreases, this held-over water starts moving northeasterly in the direction of the Bay of Fundy, engaging in a second circuit of the Gulf of Maine. Thus it enriches with plankton the

northern part of the gulf during the late summer and fall. Thus, too, the gulf is largely self-supporting, and contributes to other areas as well. The distribution of the petrel, a plankton-feeding bird, corresponds in a striking way to that of the plankton. In June and July the birds are most numerous in the southwest part of the gulf; in August they are distributed more northerly; in September they are rather evenly distributed about the gulf.

Mackerel, which are plankton-eating fish, evidently also follow a similar pattern. In early summer, they occur along the southern shores of the Gulf of Maine. By late summer they have moved to the northern shores, including the Bay of Fundy. The distribution of mackerel fishermen fits the pattern too, for of course they follow the fish.

Animals of boreal origin may be carried into the Gulf of Maine eddy, and not survive there. Thus occasionally swarms of the planktonic mollusk *Limacina retroversa* invade the Gulf. Redfield, in discussing a study of one of these invasions, writes:

> The most conspicuous result of this study is the demonstration of the degree to which the occurrence of *Limacina* in the Gulf of Maine depends upon the circulation of its waters. Damas [6] in 1905 raised the question: How does the plankton of a given region maintain its character in the face of the continual circulation of the currents and how does a given species persist so as to possess a special geographic distribution? He concluded that there must exist a special zone or center of production in which adults abound and reproduce successfully and that to this region circulatory currents serve to bring back periodically a proportion of the individuals which become entrained and dispersed by the continual movements of the water . . . The observations on *Limacina* have not revealed the presence of a center of production in the Gulf of Maine. They point to the existence of such regions offshore to the eastward and are of interest rather in telling something of the fate of these animals, entrained in the movement of water, which are carried away never to return, yet for a while to occupy an important role in the ecology of other regions. Behind the geographical distribution of each species of plankton there must be a complex balance of biological and physical factors. Of the latter, flow of water appears to be paramount; its consequences too frequently neglected.[7]

Important though flow of water may be, however, other properties of environment besides motion evidently also affect marine life, and not all of these are known. Indeed there are many mysteries about the production of marine organisms that have eluded all efforts to understand them. On a small island close to Pensacola, Florida, the United States Fish and Wildlife Service operates a laboratory for studying oysters. There, oysters taken from a homogeneous stock and planted at opposite ends of the island, a distance of not more than 1000 feet, grow at significantly different rates and

ultimately attain significantly different average size. At the same time, the growth rates in the two localities fluctuate simultaneously and in the same direction. The physical conditions at the two localities seem to be identical; at least two years of intense search have failed to disclose a difference in any measured feature of the environment.

Another example: Oysters live a brief pelagic existence during their larval stage. At length they "set"; that is, they settle to bottom, fasten to a solid object, if they happen to be lucky enough to find a suitable one, and remain there until death. The number of oysters that sets varies tremendously from year to year and from place to place. Nowhere in United States' waters has this been shown to be correlated with the number of spawners or with any of the characteristics of the sea water that have been measured in oyster beds. The degree of fluctuation itself varies. In some places, like the Thimble Islands in Long Island Sound, the oyster set is consistently good. In other places like New Haven Harbor, which is only a few miles away, it is consistently bad. Why this is so remains a mystery.

In the Limfjord of Denmark, on the other hand, scientists believe fluctuations in the set of oysters are definitely associated with weather. R. Spärck writes on this:

> The depletion of the stock of oysters on natural beds in the Limfjord . . . was not evenly distributed; in large parts of the fjord the decrease was even greater than 90 percent and it appears that in a few restricted areas the decrease was much less . . . in the period from 1925 to 1937 there was no oyster fishing at all on the natural beds in the Limfjord, so that the stock decreased only on account of natural conditions. There can hardly be any doubt that the fluctuations are mainly governed by the summer temperature since the periods of increase coincide with periods of warm summers (mean temperature in July of the surface water of the Limfjord about 18° C. or more) while periods of decrease coincide with periods of cold summers (mean temperature in July of surface water in the Limfjord 17° C. or less).[8]

The quantity of organic substances at times appears to play a most critical part in productivity of the sea. Thanks to the work of a few scientists in scattered places, evidence is slowly accumulating to foster a belief that the various organisms themselves may have important effects on each other's distribution and abundance, either by their mere presence or, more likely, by substances—ectocrines—which they impart to the water.

The literature contains many reports on the scarcity of fish in places of maximum phytoplankton concentrations. For example, R. E. Savage[9] found that *Phaeocystis,* an alga which reaches the height of its bloom in spring, sometimes seems to constitute an im-

passable barrier to the shoaling of herring on the usual fishing grounds. At other times, it may divert more herring to the fishing ground, depending on its position. Similarly, A. C. Hardy and E. R. Gunther [10] observed that in Antarctic regions euphausids and other animals of the plankton are relatively scarce where phytoplankton is abundant. They admitted that the euphausids, enormously abundant, widely distributed, and voracious as they are, must to some extent reduce the quantity of phytoplankton by grazing, a fact which can account for the observed inverse association. Nevertheless, they remarked that not only herbivorous animals of the plankton but carnivorous ones as well seemed to avoid dense patches of phytoplankton. Even the animals which were too scarce to affect the abundance of the phytoplankton appreciably by feeding on it seemed to avoid it. Hardy suggested a theory—"The Animal Exclusion Theory"—that some marine plants have properties repellent to animals and thus in effect exclude them by their presence. Biologists do not universally accept this theory, for they find it hard to believe that animals would be repelled by their food.

To test this point Richard Bainbridge,[11] working at Plymouth and Millport, studied how zooplankton behave in the presence of different species of phytoplankton. His observation aquarium consisted of a transparent tube, held horizontally for some experiments, vertically for others, and divided into compartments by sliding doors. In a typical experiment, he would fill one end of this apparatus with filtered sea water and the other with water that had been enriched with phytoplankton. Then he introduced the experimental animals in each end of the tube, opened the sliding door, and watched the animals to see the direction and speed of their migration. Did they move toward the end with the greatest concentration of phytoplankton or away from it, or were they quite irresponsive? That was the question at issue. In the horizontal apparatus there was a significant movement of experimental animals into water enriched with cultures of four out of seven species of diatoms and five out of seven species of flagellates tested. The animals did not react to three of the diatoms or to two of the flagellates tested, and they migrated away from two species of flagellates that had given evidence of having toxic properties. In several, movement toward the enriched water seemed to be more definite among the animals that had been starved before the experiment than among those that had been well fed. These experiments demonstrate that animals of the plankton react variously to different species of plants, being attracted to those which presumably are nutritious, indifferent to those which are not, and repelled by some which are distasteful or toxic. Bainbridge

concluded that phytoplankton could not remain abundant long in the presence of herbivorous animals. The suggested sequence of events is something like this: on locating a concentrated stand of plants a swarm of animals feeds until it has reduced it almost to the vanishing point; then it goes searching for another pasture. Thus plants can remain in dense aggregation only until animals find them, and thus the exclusion effect is produced. Bainbridge suggested that the positive or negative reactions which certain species of plants invoke among animals might be mediated by substances excreted into the water.

Scientists have known for a long time that sea water contains considerable quantities of dissolved organic substances.[12] These are presumably the products of decomposition of the dead bodies of plants and animals and of the processes of respiration, secretion and excretion of the living. For the past twenty-five years, biologists have accepted Krogh's [13] contention that these substances are not used as food in the ordinary sense, at least the metazoan animals do not seem to take up significant quantities of them. Yet a number of pieces of evidence from recent studies suggest that organic substances in sea water *are* biologically important to living organisms, if not actually used as food.

It is simple to make up an artificial sea water with the proper proportions of the various chemical constituents dissolved in distilled water. This can be enriched with phosphate, nitrate and iron, and its hydrogen ion concentration can be adjusted with carbonate, so that by ordinary chemical tests it is indistinguishable from natural sea water. Nevertheless, certain species of diatoms will not grow in it until some natural sea water is added; only a small amount is enough to start the plant culture growing vigorously. The same effect can be produced with a decoction of algae, or with soil extract, or with certain organic compounds. Not all natural sea water has this life-stimulating property. For example, water which H. W. Harvey collected near Plymouth in late summer and early autumn of 1937 and again in July 1938, lacked it, as evidenced by the fact that diatoms did not grow in it but formed spores which failed to develop and died in spite of the water's being fertilized with inorganic nutrients. On the other hand, two lots of water which Harvey collected in the same place in October 1937 and April 1938 proved to be fertile enough for diatoms to grow in without the benefit of organic additions. Harvey then concluded:

> The inference drawn from these observations on growth in natural sea water is that these two particular strains . . . require for continued growth, not only a supply of available nitrogen, phosphate and iron, but in addition, some

other accessory substance or substances, whose concentration in offshore sea water was less than the necessary limit during the summer of 1937 and 1938. In the autumn of 1937 either the accessories were re-formed or a body of water containing the accessories had moved into the area. This *"fertile water"* either lost its fertility or was gradually replaced during the early summer of 1938. Samples of offshore water collected during the autumn and winter of 1938 behaved in the same way as water collected during the summer—there was no return of "fertile water." [14]

These accessories are evidently a complex of substances which Harvey has divided into two groups, *A* and *N*. The biological effects of *A* substances on diatoms can be duplicated by adding *l*-cystine, glutathione, methionine, aneurin (Vitamin B_1), or biotin. There is probably some special biological significance to the fact that these compounds all contain divalent sulphur. Water rich in accessory *A* substances becomes infertile on standing and will not support diatoms until fresh *A* substance has been added. The effects of *N* substances can be duplicated in part by certain other compounds, among them *dl-α* amino-propionic acid, *dl-α* alanine, *dl* lactic acid, dextrose, and gluconic acid, all of which form complexes with iron and manganese. Diatoms will grow in sea water enriched with nitrate, phosphate, and iron, without any accessory substance, provided a small amount of manganese is present. They grow better if silica and trace elements are also present, but still better when accessory substances are added.

For many years the staff of the Plymouth Laboratory had measured the annual cycle of nutrients and of the resulting abundance of plankton and young fish in the English Channel near Plymouth. During the winter of 1930 there occurred a sharp drop in the concentration of phosphate, which was followed shortly by a drop in the abundance of plankton and young fish, and a disappearance of the herring that had formed the basis of an important winter fishery. At the same time, the composition of the pelagic fauna changed. Whereas for five years a certain arrowworm *Sagitta elegans* had been the more prominent of the two principal species of the group of animals which occurs in that part of the world, it was replaced by another species of arrowworm, *Sagitta setosa,* which has predominated almost continually ever since. Each of the two worms is associated with a particular environment, *S. elegans* with a body of water ("western water") coming from the direction of the open Atlantic, and *S. setosa* with the water of the English Channel. Under favorable oceanographic conditions, western water has pulsed seasonally into the channel carrying with it its characteristic fauna. Some scientists affirm (others disagree, or at least consider unverified) that channel water is favorable for a flowering of the diatom

Rhizosolenia, which in turn seems to repel herring. It is unfavorable to the survival of larvae of certain sea urchins and Polychaete worms. Under laboratory conditions these young animals developed abnormally when nurtured in channel water, but in water identified at sea as "western" and transported to the laboratory, they prospered and grew normally.

One of these bodies of water must contain some substance still unidentified which the other lacks. This substance may be necessary to the production of living organisms, and therefore a constituent of western water. On the other hand, it may be toxic and a constituent of English Channel water. Douglas Wilson has carried out experiments pertinent to this problem. He finds that worm larvae do not live in a jar of pure channel water; on the other hand, they do very well in a jar of western water. The addition of some western water to the jar of channel water evidently adds whatever is needed for the survival of the worm larvae. So it appears that the western water does contain some symbiotic substance.[15]

On the other hand, sea water also contains antibiotic substances which under some circumstances may be enormously important. To non-marine bacteria, sea water is curiously antagonistic. They cannot be cultivated on nutrient agar prepared with it. It kills 80 per cent of the organisms in sewerage within half an hour. The salt is not what kills the organisms, nor the osmotic pressure, as proved by the fact that after the water is heated bacteria will live in it almost indefinitely even though it is no less salty than before. Besides, they will grow on media made of artificial sea water. Evidently there is something in the natural water that has an antibiotic effect. What this something is has not yet been determined. It deteriorates on standing, some but not all of it is stopped by fine filters, and it is destroyed by heat. Its effect is strongest in fresh sea water collected in places where the population of marine bacteria is most concentrated. Among fifty-eight species of marine microorganisms which William Rosenfeld and Claude ZoBell [16] tested at Scripps Institution of Oceanography, nine were found to exert an antibiotic effect against non-marine forms.

B. H. Ketchum and others of the Woods Hole Oceanographic Institution observed the same effect in nature.[17] At Mount Hope Bay, Massachusetts, they found that the concentration of coliform bacteria discharged in domestic sewerage diminishes much more rapidly than can be accounted for by mere dilution with sea water. Again in New Jersey, Ketchum and his colleagues [18] studied the fate of coliform bacteria in the Raritan River and its tidal estuary. They began at a point where the bacteria, recently introduced into the

river, numbered 115,000 per cubic millimeter, and they made comparable observations successively toward the mouth of the river until the concentration of cells reached 214 per cubic millimeter. Almost all of the diminution in concentration was accounted for by the joint action of dilution, antibiotic effects, and predation. In the river end of the estuary, the three were about equal in their effect, but toward the sea the bactericidal action gained ascendancy until at the end of the observations it was about thirty-five times as effective as dilution and about sixteen times as effective as predation in reducing the concentration of the bacteria.

In a review of the significance of organic substances in sea water, C. E. Lucas, of the Scottish Marine Laboratory at Aberdeen, Scotland, writes:

> Here may briefly be considered the possible mediation of "animal exclusion" in which it now seems reasonable to see the more or less passive avoidance of certain plant products [those typical of peak numbers] which in some instances may prove lethal if they cannot be avoided. . . . The widespread occurrence of antibiotics elsewhere makes highly probable the existence of such processes in the sea, and a diversity of processes may be anticipated. Some of them may only apply between some plants, and others only between some animal species, whilst "antibiotics" between some organisms may prove to be "symbiotics" between others. In the case of "animal exclusion" the observed effect is between plants and animals (i.e., the plants inhibiting the the animals, although it is by no means certain that instances of the reverse inhibition do not occur, in view of the known excretion by animals of substances of biological significance). The nature of the metabolite in "animal exclusion" is as yet quite uncertain; it is possible, however, to suggest one type of agency, although by no means the only possible one. . . . Phytoplankton organisms produce carotenoids and sterols within their bodies, and their flowerings are known to leave large quantities of the former and probably of the latter, by one means or another free in the water. . . . The comparatively well-established knowledge of the influence of sterols in life, and the growing appreciation of that of the carotenoids, immediately suggest their probable significance as free environmental agents. . . .
>
> Whilst certain carotenoids and sterols, at moderate concentrations, might well be beneficial to certain animals, at higher concentrations they might induce avoiding reactions or be lethal.[19]

Thus the abundance and distribution of any species in the sea, including those useful to man, are influenced in varying degree and in various ways by all the other kinds of creatures about them. Where there is a rich production of phytoplankton, there can be expected to follow a rich production of zooplankton and thence of higher invertebrates, fishes, and marine mammals. But these relations are evidently not so simple that they can be described in a system of formulations such as the gas laws. Some species of phytoplankters can prosper only in water in which other phytoplankters

have preceded them. Other species are less demanding. Phytoplankters give off substances which have important physiological effects on animals, some favorable and attracting, others unfavorable and repelling, still others deadly poisonous (see Chapter 11). At least one species of animal, the American oyster, and therefore perhaps others, seems to be able to feed only when dissolved organic substances exceed a certain critical concentration.[20]

How important to the well-being of fishery stocks are these organic substances that have biological effects? What are the mechanisms of their physiological actions? What controls the rates of their formation? What is the geography of their distribution? These are questions which will be answered only with the accumulation of a great deal more knowledge than exists today about the biochemical and physiological intereffects of organisms. They are questions which might be most fruitfully studied by an environmental laboratory.

Thus a fishery stock in an environment is but one detail in a vastly intricate system. Biologists usually refer to the predator-prey relations in this system as "the food chain," evoking thereby an image of an orderly succession of linkages, connecting smaller fodder to feeders, that is, microscopic plants to herbivorous plankters to small carnivores to successively larger ones. Although this is a useful piece of jargon, the scheme of things in the sea cannot be adequately described as a chain. "The food pyramid" is an expression that is frequently used; "the web of life" is another, "cycle of life" still another. Whatever we call the system, however, the primary element in it is the array of microscopic organisms which fulfill many functions, of which the most obvious are the synthesis of carbohydrates by plants and the dissolution of dead organisms by bacteria.

Diatoms, flagellates, protozoa, and bacteria are the most numerous organisms in the sea and the groups about which least is known. Furthermore they are the least studied. This is less true of diatoms than of the other groups. Diatoms are easily collected, preserved, and identified, and their functions seem fairly clear cut. Ecologists in discussing the food pyramid emphasize the diatoms as the chief primary producers because they are the most familiar. At the same time, the naked flagellates, which photosynthesize, may be quite as numerous and as important. These organisms are exceedingly delicate; they disintegrate in preservative and therefore it is difficult to sample them quantitatively. For example, *Gymnodinium brevis*, a dinoflagellate, is killed within seconds if the collecting apparatus contains a trace of copper, to which it is particularly sensitive. Bacteria are affected similarly by metals, as may be species of

flagellates other than *G. brevis.* Consequently present ideas of the abundance of these organisms may be based on gross underestimations.

What is the role of dinoflagellates in the sea? They photosynthesize, and under some circumstances they also ingest food. They can use extremely low light intensities in photosynthesis. Could it be that they are the chief primary producers in deep water? In this connection it may be especially significant that they can apparently live at lower nutrient levels than many other microscopic forms, such as diatoms.

Bacteria are widely distributed and extremely important in marine ecology. They too are closely involved with fundamental processes in the sea. Yet there are few scientists engaged in marine bacteriological research. ZoBell in his monograph on hydrobacteriology writes, "It has been necessary to rely largely upon personal judgment in recording the frequency of occurrence of bacterial genera in the sea. The descriptions of many marine bacteria are so fragmentary that it is difficult or impossible to ascertain the genus to which they belong." [21] The biology of microorganisms of all classes has been more neglected than any other subject of marine research. Work in this field should be greatly expanded to include laboratory physiological and biochemical studies as well as careful quantitative observations at sea.

How observations on characteristics of the environment might be integrated to evaluate the role of each element and to predict biological effects under given circumstances has been demonstrated by Riley, Stommel, and Bumpus in an analysis of data concerning a portion of the western North Atlantic Ocean.[22] They took into account measurements of solar radiation, temperature, vertical turbulence, transparency, and the concentration of phosphates in deep water; and they used these five environmental factors to estimate theoretical quantities of phytoplankton, herbivorous zooplankton, and carnivorous zooplankton. The quantities of plankton which they estimated for various parts of the western North Atlantic corresponded closely to the quantities which they actually observed during the brief period of their study. As more systematic data about environments accumulate, the accuracy of such estimates should improve. Furthermore, it might become possible to extend the methods to the prediction of the abundance of fishery stocks.

In the foregoing pages, I have tried to develop a case for setting up teams of scientists to concentrate their attention on the study of marine environments. It must be admitted that a considerable body of theory and fact on this subject has already accumulated for a

number of regions. Indeed, it is not possible to carry on any serious marine oceanographic or fishery study without adding to knowledge about environment. A few scientists in scattered places devote all their time to integrating data in order to formulate a concept of environmental dynamics. Gradually, their efforts should become ever more rewarding and useful. Still, these people depend very largely on hand-me-down data. They have little to work with and little help, and their inclusion in oceanographic programs, while welcome, is often pointedly incidental to other activities. Consequently the growth of knowledge about sea environments is retarded.

The literature is full of comparisons between the productivity of the land and of the sea, between farming and fishing. There really is no adequate basis for comparison yet; we do not really know the sea as we do the land, and our knowledgeable use of sea environments is centuries behind that of land environments. If it were desired to expand knowledge about marine environments, where it is most needed, what would be the best way of going about it? The most obvious answer would seem to be this: Establish laboratories in maritime countries where they are now lacking. It would seem logical to give precedence to countries whose populations are densest, whose food problems are most serious, whose fisheries are still far undeveloped, and which are within practical cruising range of promising fishing grounds.

This seems reasonable enough. If there are so many laboratories in northern countries, they must be needed. If they were not beneficial or at least gave no promise of being beneficial, they would not continue to be supported as they are. If they are needed in one part of the world, why not also in another?

However, it is easy enough to say, "Put marine laboratories here and there." Some serious obstacles have to be faced. These institutions cost a great deal of money to establish and a great deal more to maintain. The laboratory building is only the beginning. There must ultimately be expensive equipment such as aquaria, scientific instruments, libraries, fishing gear, and sea-going vessels. There must be a well-balanced staff of scientists who are paid salaries high enough to keep them happily attached to the institution, and given enough expense money to make their research programs effective. It is better not to establish a laboratory at all than to give it poor equipment, inadequate support, and half-hearted backing.

Money, then, is the first problem. However, it is not necessarily the most difficult one. Recruiting the scientists might be harder.

These men should be well educated in their fields. The director of a new environmental research laboratory situated in a relatively unexplored area should have an exceptionally wide range of learning and experience. His team should be composed of men dedicated to applying their several fields of learning to the central goal of understanding the sea as a system of environments for living organisms. Drawn from many countries, they should be congenial and understanding of each other's cultures. Scientists willing to uproot themselves are not easily found. Apart from that fact, there are not enough qualified general marine biologists, fishery biologists, and physical oceanographers in the world to satisfy present demands. There is some hope that this situation will improve, since many countries are sending students to northern universities for training in aquatic sciences. Yet here another problem is introduced. These people go to long-established, well-equipped research centers for their education. They become familiar with advanced techniques. When at length they return home, ready to begin putting their learning to use, they often find nothing to work with—no suitably equipped laboratory, not enough money to finance a research program, a vessel perhaps, but no means to operate it, and worst of all, only half-hearted interest from their government. Sometimes a man returns home to find his job gone. These are the most frequent complaints of foreign students in northern universities. Probably it is unreasonable to expect large enough means to maintain an effective laboratory in every country. The alternative, of course, is to encourage two or more countries to cooperate in establishing and maintaining regional laboratories.