CHAPTER VIII

The Sea as a Biological Environment

In the foregoing chapters an account has been given of the chemical and physical aspects of the elements that together constitute the inorganic marine environment—namely, (1) the sea water itself, and (2) the ocean floors. The chemical constituents and the physical properties of the sea water, together with their distribution, concentrations, and cyclic changes, the movement of the water, and the nature of the ocean floors are decisive factors in the history and fate of a perplexing array of living things. Herein are held many secrets of racial development, and herein must be sought the understanding of the delicately balanced maintenance of life and of the potentialities of future development.

Marine organisms are to be considered a part of the sea as it exists today. Just as sea water includes the various salts, both conservative and nonconservative (biologically changed), so also it includes the multitude of organisms which are bound to the sea for their existence and which, by origin, are a part of the sea both racially and individually. The organisms, like the salts, are subject to the natural laws of the sea and are a part of the perpetual cycle of inorganic and organic substances so important in many aspects of oceanography. The changes that are apparent in concentration represent only patterns that are inherent in the phases of the cycle or that result from other causes, such as currents and processes of mixing.

The aquatic environment offers the greatest intimacy between itself and the organisms which it bathes both over the body surface and within open or partially closed cavities as, for example, the internal systems of coelenterates, echinoderms, and tunicates. Because of the stability of the physical characteristics of the sea water and of the composition and concentration of the dissolved salts the organisms, in general, have not developed highly specialized integuments and regulatory systems to protect themselves against sudden and intense environmental changes, as have most land animals. It follows that small changes in the aquatic medium are promptly brought to play upon its population. It should be borne in mind, also, that the organisms themselves, being a part of the dynamic environment, modify particularly its chemical character by withdrawing or adding substances associated with the activities of life.

In subsequent chapters we shall discuss the relation of some of the measurable environmental factors to such phenomena as distribution, propagation, survival, and special adaptations, but first some facts of general application must be considered.

Physical and Chemical Characteristics of the Marine Environment

Water is essential to the maintenance of all life. It constitutes 80 per cent or more by weight of active protoplasm. It is the *most efficient of all solvents* and carries in solution the necessary gases, oxygen and carbon dioxide, as well as the mineral substances necessary to the growth of plants and animals, and it is itself one of the *essential raw materials* in the manufacture of foods by plants.

Organisms living in the terrestrial environment have devised means, such as impervious integuments, to conserve water, and the land plants have roots and special vascular systems for transport of water to all growing parts. In the marine environment there is *freedom from dessication*, except at high-tide levels, and therefore no highly specialized means are provided for conservation of water or for its transport in plants.

Also of biological importance are the high *heat capacity* of water and its *high latent heat of evaporation*, both of which obviate the danger that might result from rapid change of temperature in the environmental medium. Owing to the high degree of *transparency* of water it is possible for the sea to sustain plant life throughout a relatively deep layer, and in animals the development of organs of vision and of orientation has progressed to a marked degree.

Sea water is a *buffered solution;* that is, changes from acid to alkaline condition, or vice versa, are resisted (p. 195). This property is of vital importance to the marine organisms, mainly for two reasons: (1) an abundant supply of carbon can be available in the form of carbon dioxide for the use of plants in the synthesis of carbohydrates without disturbance to the animal life that may be sensitive to small changes in *p*H, and (2) in the slightly alkaline habitat the many organisms that construct shells of calcium carbonate (or other calcium salts) can carry on this function much more efficiently than in a neutral solution.

The support offered to the bodies of marine organisms by the specific gravity of the surrounding medium obviates the need of special supporting skeletal structure in many forms. Striking examples of these are the jelly fishes, unarmored molluscs, unarmored dinoflagellates, and even the large marine mammals with their heavy skeletons, which could not survive in their present bulky state except in an aquatic habitat. The hard shells of crabs, clams, snails, and so on, doubtless serve as support, especially in some burrowing and intertidal forms, but these hard parts may be looked upon also as protective and as a framework for attachment of muscles used in digging, creeping, or swimming.

Sea Water and the Body Fluids. Sea water is a most appropriate environment for living cells, since it contains all of the chemical elements essential to the growth and maintenance of plant and animal protoplasm. It has been shown that sea water is a solution of a large number of salts, and it is important here to consider how it is related as an external fluid medium to the "internal medium"—namely, the body fluids (blood, coelomic fluid, and so on) of the organisms. The ratios of the major salts to each other, and usually their total concentration also, are strikingly similar in sea water and in the body fluids of marine invertebrates. The similarity of composition is not confined to marine animals, however, but is also in evidence in modified form in both terrestrial and fresh-water animals, including the lower and higher vertebrates, as is shown in table 55, which is from data compiled by Pantin (1931) and expanded by Dakin (1935).

Osmotic Relationships. It is well known that when solutions of different osmotic pressure are separated by a semipermeable membrane that allows the passage of water but not of the solutes, there is a movement of the water through the membrane into the more concentrated solution. The cell membranes of organisms are just such semipermeable membranes through which a movement of fluids occurs inward or outward, depending upon whether the osmotic pressure of the external medium is less (*hypotonic*) or greater (*hypertonic*) than the internal medium. The internal and external media are *isotonic* when they are of equal osmotic pressure.

The osmotic pressure of a solution can be computed from the freezing-point depression (p. 67). This computation is possible because the salts that increase the osmotic pressure of a solution also depress its freezing point. The freezing-point depression below 0°C has been designated by $\Delta\vartheta_f$ (p. 67), but will here be abbreviated to Δ. Sea water having a salinity of 35.00 $^0/_{00}$ freezes at $-1.91°$, owing to depression by the substances in solution. In other words, the value for Δ is 1.91°. Similarly, we obtain a Δ of 0.56 for human blood with a freezing point of -0.56°C.

On the basis of Δ values, the osmotic relations of the body fluids of marine and fresh-water animals to their external environmental medium are compared in table 56, from data compiled by Dakin (1935), to whose review the reader is directed for much greater detail and historical treatment.

From the few examples in the table it is evident that the body fluids of marine invertebrates are isotonic or nearly so with their fluid environment, whereas in the fresh-water forms the body fluids are hypertonic to the dilute external medium. For this reason the marine environment in its osmotic relations fails to exact of its inhabitants as great an expenditure of energy in maintaining the proper concentration of body

TABLE 55

THE COMPOSITION OF SEA WATER AND THE BODY FLUIDS OF VARIOUS ANIMALS

(After Pantin, 1931, and Dakin, 1935)

	Date taken or calculated from	Na	K	Ca	Mg	Cl	SO_4
Sea water	....	100	3.6	3.8	12.1	180	25.2
Aurelia flavidula (*mesogloea*)	Macallum (1926)	100	5.2	4.1	11.4	186	13.2
Limulus polyphemus	Macallum (1926)	100	5.6	4.1	11.2	187	13.4
Aplysia limacina	Bethe (1929)	100	4.0	4.4	11.0	180	
Homarus americanus	Macallum (1926)	100	3.7	4.9	1.7	171	6.7
Acanthias vulgaris	Macallum (1926)	100	4.6	2.7	2.5	166	
Carcinus maenas	Bethe (1929)	100	4.8	4.5	4.8	180	
(Cod) *Gadus collarus*	Macallum (1926)	100	9.5	3.93	1.41	149.7	
(Pollock) *Pollachius virens*	Macallum (1926)	100	4.33	3.10	1.46	137.8	
Frog	Macallum (1926)	100	11.8	3.17	0.79	135.6	
Dog	Macallum (1926)	100	6.6	2.8	0.76	139.5	

fluids as does the fresh-water environment. The exact mechanism whereby the fresh-water animals are independent of the external medium and are able to maintain a *homoiosmotic* condition (that is, steady value for Δ) in the presence of the hypotonic water is not known (see Δ for the eel *Anguilla anguilla* in fresh and salt water, table 56). Their existence under these conditions, however, requires a constant expenditure of energy in eliminating, through the kidneys and other excretory organs, the excess water taken in by osmosis. Marine invertebrates are *poikilosmotic* (Δ changing with that of the external medium) only within rather narrow limits (Dakin, 1935); hence, they, too, must have some regulating mechanism. Except in estuarine conditions, however, the range of salinity in most parts of the sea is perhaps within the limits of poikilosmoticity of the invertebrates living there. For example, the lugworm, *Arenicola marina*, in Helgoland waters with a $\Delta 1.72$ has an internal medium $\Delta 1.7$, but in the Baltic Sea with a water of $\Delta 0.77$ the same species has a Δ value of 0.75 for the internal medium.

It should be mentioned here that the teleost (bony) fishes in marine waters are definitely hypotonic and, therefore, in order to keep their body fluids down to the required osmotic pressure for the species, they secrete chloride through the "chloride cells" of the gills (Keys, 1933). This function is a regulation toward a low osmotic pressure of the blood, as opposed to regulation toward a high one as performed by the kidneys of animals in fresh-water environments. That this group of aquatic animals has achieved a marked degree of independence of the osmotic pressure of the external medium is evidenced especially by such forms as the salmon and eel, both of which, though practically homoiosmotic, spend their lives partly in hypotonic and partly in hypertonic environments. The elasmobranchs—namely, the sharks and rays—are isotonic with sea water, but in these the high osmotic pressure of the blood is due not only to the presence of such salts as occur in sea water, but also to high urea content. For further discussion of salinity as an environmental factor, see also p. 839.

Other Characteristics of the Environment

In addition to the chemical and physical properties of sea water, certain other biologically important characteristics are inherent in the marine environment as a whole. These result from the magnitude of the ocean itself, its great depth, and its expanse.

In considering the ocean in its entirety as an environment, we are at first impressed by the wide ranges of living conditions, the salinities varying from those of dilute estuarian waters to concentrations of 37 $^0/_{00}$ or more in the open sea, temperatures from 30°C to freezing point, light intensities from brilliant sunlight at the surface to absolute and perpetual darkness in the deeper layers, and pressures from a single

TABLE 56

COMPARISON OF CORRESPONDING VALUES OF Δ OF INTERNAL AND EXTERNAL MEDIA OF CERTAIN MARINE AND FRESH WATER ANIMALS

(After Dakin, 1935*)

Marine Animals			Fresh-water Animals		
Species	Internal medium Δ°C	External medium Δ°C	Species	Internal medium Δ°C	External medium Δ°C
Annelida			Mollusca		
Arenicola marina	1.72	1.7	*Anodonta cygnea*	0.09	
Arenicola marina	0.77	0.75	*Unio pectorum*	0.15	
			Limnaea stagnalis	0.22–0.23	0.02–0.03
Mollusca					
Ostrea edulis	2.23	2.11–2.14	Crustacea		
Mytilus edulis	2.26	2.11–2.14	*Telphusa fluviatile*	1.17	
Octopus vulgaris	2.16	2.11–2.14	*Daphnia magna*	0.20–0.67	
			Potamobius astacus	0.80	
Arthropoda			*Eriocheir sinensis*	1.09	
Homarus americanus	1.82	1.80	*Astacopsis*	1.1	
Cancer pagurus	1.84–1.91	1.91			
Hyas aranea	1.83	1.80	Teleost fishes		
Limulus polyphemus	1.90	1.82	*Salmo fario*	0.57	
			Anguilla anguilla	0.62	
Tunicata			(in sea water)	0.73	1.87
Ascidia mentula	2.08	1.98	*Barbus fluviatilis*	0.50	
			Cyprinus carpio	0.50	
Teleost fishes			*Anabas tetudineus*	0.64	
Pleuronectes platessa	0.787	1.9			
Conger vulgaris	0.77	2.14	Dipnoi fishes		
Gadus aeglefinus	0.74	1.92	*Epiceratodus fosteri*	0.42	

* Dakin includes certain observations from the region of Naples giving the Δ of the sea water as 2.29°. These observations, which are often quoted in the literature, have been omitted here because a Δ of 2.29° corresponds to such a high salinity (43.5 ‰) that it must be in error. The maximum salinity in the western Mediterranean is about 39 ‰ and the corresponding Δ is 2.14°.

atmosphere at the surface to about 1000 atmospheres in the greatest oceanic deeps.

Impressive as these ranges may be, nevertheless very uniform conditions do prevail over extensive areas of the environment, and many organisms may, by reason of the monotony of these extensive areas, be very delicately attuned to the prevailing unvarying conditions. Hence, it follows that faunal areas characterized by specific forms can be recognized. On the other hand, a wide range of conditions may be encountered in more restricted areas, especially in coastal regions. These conditions may be due to the physiographic character of the coastline, depth to bottom, topography and nature of the bottom, inflow of land drainage, meteorological conditions, and so forth. Specially adapted and tolerant forms occur here in profusion, for, as will be shown in later chapters, the shallow depths and varying conditions are frequently favorable to abundant production of primary food.

It must not be overlooked that the gradients of salinity, light, and temperature that exist in the sea are favorable to a number of sensitive animals that possess the ability, through swimming or otherwise, to adjust themselves to optimum conditions.

DEPTH AND LIGHT. Inherent in the vertical range or depth of the open-sea habitat are a number of important features of far-reaching biological effect. Of prime importance is the relatively great vertical range of the euphotic zone available for production of floating microscopic plants. But the gradient of light, both as to quantity and quality, resulting from depth of water also allows adjustment of many animals to the optimum condition with respect to this factor and, indeed, is associated with diurnal migrations of many forms to lighter or darker situations.

PRESSURE. Pressure in itself does not exclude life from the abyssal regions of the sea, for water is but little compressed and equilibrium exists between the inner and outer pressure affecting the body tissues. However, pressure may limit the vertical range of motile forms, although some eurybathic animals apparently are not seriously affected and are known to make daily vertical wanderings of up to 400 m, corresponding to pressure variations up to 40 atmospheres. Harpooned whales are said to "sound" to a depth of 800 m, and the sperm whales must descend normally to great depths, since the large squids upon which they feed inhabit very deep water.

WATER MOVEMENTS. The sea must be viewed as an environment that for the most part is in constant motion with both regular and irregular patterns of flow. The principal biological benefits derived from the circulation are (1) oxygenation of subsurface water, (2) dispersal of wastes resulting from processes of metabolism, (3) dispersal of plant nutrients and other variable elements essential to plant and animal growth, and (4) dispersal of spores, eggs, larvae, and also many adults. On the whole, the circulation of water is of direct benefit, yet instances may be noted where some adverse conditions result either as incidental or as permanent features. Incidental disturbances may be due to unseasonable shifts in the regular current system, such as give rise to the appearance of "El Niño" off the west coast of South America (p. 704). In this instance, warm water of the Equatorial Countercurrent is carried southward along the coasts of Ecuador and Peru, which are normally bathed by cold currents. The result is a wholesale destruction of animal life along the coast, including many guano birds that depend upon the sea for food. Permanent or semipermanent features of current systems that take a regular toll of life are found where the moving water carries the inhabitants into areas of less favorable living conditions. For example, Gulf Stream inhabitants ultimately perish as they are swept northward into regions where the temperature of the water is lowered by admixture of cold water or by cooling in higher latitudes. Larvae of neritic forms are frequently dispersed to offshore or other locations uninhabitable to the adult animals. Surface currents sometimes strew the shores with defunct bodies of normally oceanic or offshore forms such as the coelenterate *Vellela* or the pelagic snail *Janthina*.

EXTENT OF THE MARINE ENVIRONMENT. That part of the earth which is capable of sustaining life, both plant and animal, is known as the *biosphere*. The biosphere is subdivided into three principal divisions or habitats known as *biocycles*. These are the terrestrial, the marine, and the fresh-water biocycles. Each has its characteristic types of ecological features and associations of plants and animals. A few animal species may at times migrate freely from one to another, as is witnessed especially by the salmon or the eel.

The oceans cover some 71 per cent of the earth's surface. Thus, the area of the oceans is about two and one half times the area of the land, but, when considering the space in which life might conceivably exist, account has to be taken of the relative vertical range provided by the two main environments, the terrestrial and the marine. On this basis it is estimated (Hesse, Allee, and Schmidt, 1937) that the marine environment actually provides about three hundred times the inhabitable space provided by the terrestrial and the fresh-water biocycles together; for, whereas the terrestrial environment provides space only in a shallow zone mainly at the immediate surface and to a depth of a few feet at the most, the marine habitat provides livable space for at least some form of life from the surface even to the abyssal depth of several miles. The fresh-water biocycle constitutes only a small fraction of the other two. The aerial portion of the globe is not properly considered a separate biocycle, since entrances into it by birds, insects, and so forth may be considered mainly as temporary journeys.

Owing to the difficulties attendant on the study of the oceans, the marine biocycle is the least known of all.

Classification of the Marine Environment

In order to facilitate a study of the marine environment and its inhabitants, the former may be conveniently divided broadly into primary and secondary biotic divisions based upon physical-chemical attributes or upon the nature of the biota. The boundaries between these biotic

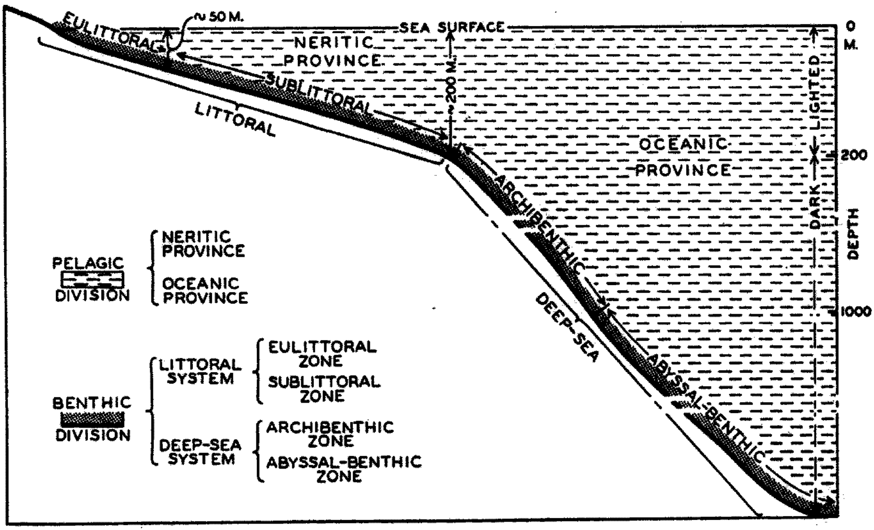

Fig. 67. The main divisions of the marine environment.

divisions, which are diagrammatically shown in fig. 67, are in some instances well defined, but more frequently there is a good deal of overlapping. Thus, although the primary divisions are definitely set off from each other on physical bases, and the typical subdivisions of these habitats can be clearly recognized both biotically and abiotically, yet there are no well-defined boundaries between them.

The two primary divisions of the sea are the *benthic* and the *pelagic*. The former includes all of the ocean floor, while the latter includes the whole mass of water.

The Benthic Biotic Environment and Its Subdivisions. This division includes all of the bottom terrain from the wave-washed shore line at flood-tide level to the greatest deeps. It supports a characteristic type of life that not only lives upon but contributes to and markedly modifies the character of the bottom. Ekman (1935) discusses the boundaries of the vertical zones from a zoogeographic standpoint, and we follow mainly the scheme employed in his text.

The benthic division may be subdivided into two main systems—namely, the *littoral* and the *deep-sea systems*. The dividing line between these has been set at a depth of about 200 m on the arbitrary supposition that this represents the approximate depth of water at the outer edge of the continental shelf (p. 20), and, roughly, also the depth separating the lighted from the dark portion of the sea. The littoral system is subdivided into the *eulittoral* and the *sublittoral* zones. The deep-sea system is divided into an upper (*archibenthic*) and a lower (*abyssal-benthic*) zone. The limits of the benthic subdivisions are hard to define, and are variously placed by different authors because uniform boundaries that will fit all requirements cannot be drawn. For general biological studies, the different boundaries must be based on the peculiarities of the endemic plant and animal distribution and should follow the region of most distinct faunal and floral change. The biotic zones thus delineated will be characterized by a more or less clearly defined range of external ecological factors which have given character to the population.

The eulittoral zone extends from the high-tide level to a depth of about 40 to 60 m. The lower border is set roughly at the lowest limit at which the more abundant attached plants can grow. The sublittoral zone extends from this level to a depth of about 200 m, or the edge of the continental shelf. The dividing line between these subdivisions varies greatly between extremes, since it is determined by penetration of light sufficient for photosynthesis. It will be relatively shallow in the higher latitudes and deep in the lower latitudes. In the upper part of the eulittoral zone a relatively well-defined tidal or *intertidal* zone that is bounded by the high- and low-water extremes of the tide is recognized. Some authors confine the eulittoral zone to this narrow section and consider the sublittoral to begin at the low-tide level (cf. Gislen, 1930). The vertical range of the intertidal zone, though rather well defined for any given area, varies greatly in different sections of the world, for it is determined by the tidal range (see chapter XIV). In the upper reaches of the Bay of Fundy the zone may have a vertical range of over 15 m, while in the Gulf of Mexico it is less than 0.7 m, and in areas like the Mediterranean along the southwest coast of Italy the range is yet smaller, only 10 to 30 cm. On exposed coasts subjected to direct ocean waves and swells the upper range is somewhat extended to include a rather well-defined supratidal spray zone with a sparse population of especially resistant forms among which a few animals, such as the isopod *Ligyda*, appear to be in the process of becoming terrestrial in habit. Many species of animals are found only in the tidal zone and may be limited vertically in maximum distribution even to certain levels within the zone—for example, *Ligyda* and the gastropods *Littorina scutalata, L. planaxis*, *Acmaea digitalis*, and others found at Monterey Bay only above the 0.76-m tidal level (Hewatt, 1937). Thus, in the tidal zone in which the range in external factors is greatest we find a more restricted vertical range of specific animals than is obvious anywhere else in the benthic region of the sea. Many motile animals, for example crustaceans and fishes, move regularly into the intertidal zone to feed during high tide, and the small pelagic fish known as grunion migrate into the zone during certain high spring tides to deposit their eggs in the sand.

The eulittoral zone gives rise to many biotopes, for it is greatly varied as to type of substratum—for example, rocky, sandy, or muddy—and also as to character of shore line and degree of exposure. The overlying water may be slightly or greatly reduced in salinity. These variations are direct, decisive features controlling the type and abundance of sessile littoral forms (cf. Shelford *et al*, 1935). The plentiful primary food in this zone is derived from both pelagic and attached plants.

Attempts to establish such zones as Fucus zone, Laminarian zone, and so on, based on the depths at which these plants are characteristically attached, has the disadvantage that the plants are very frequently absent along vast stretches of the coast, owing to unfavorable substratum or other ecological factors; nevertheless, such classification may be of useful local application.

Though the boundary between the sublittoral and the deep-sea systems is set at a depth of 200 m, Ekman's compilations based on the fauna indicate that in most regions the boundary may be located between 200 and 400 m. Light and temperature are important factors, and in high latitudes these factors operate together to shift the boundary into shallower water.

The upper division of the deep-sea system is called the *archibenthic*, a word introduced by Alexander Agassiz, but the term is unfortunate in that it implies the beginning of the benthos from this region. The zone is also called the *continental deep-sea zone*, but this gives rise to greater confusion, since the term "continental fauna" sometimes used must include also the littoral fauna unless specifically called *continental-slope* or *deep-sea* fauna. The *archibenthic zone* extends from the sublittoral to a depth between 800 and 1100 m.

The *abyssal-benthic zone* comprises all of the deep-sea benthic system below the archibenthic zone. It is a region of relatively uniform conditions. Temperatures are uniformly low, from 5° to −1°C, and solar light is wanting. There are no seasons, and hence the seasonal biological phenomena associated with the littoral zone are suppressed. Stagnant conditions do not prevail in the open ocean, however, for there is ample circulation to supply well-aerated water resulting from deep vertical movements in the high latitudes (p. 138). No plants are produced, and the extent to which autotrophic bacteria play a part in the manufacture of food is not known. The animals are carnivorous, feeding mainly upon organic detritus which in its initial organic state must have originated in the plants of the surface waters. The abyssal zone, though not sharply marked off at its upper limits from the archibenthic zone, has its own characteristic population, as will be brought out in a following chapter.

The benthic environment from shore seaward to abyssal depths is covered, to a greater or less degree, by sedimentary deposits that may be classified as terrigenous deposits, organic or pelagic oozes, and red clay. A detailed discussion of the deposits will be found in chapter XX, and the nature of the distribution is shown in fig. 253. As far as the biology of benthic animals is concerned, the most important features of these oozes are their physical consistencies and the amount of digestible organic material they contain. Most deep-sea benthic forms are detritus eaters and mainly dependent, therefore, upon the rain of pelagic organisms that falls to the bottom. The production of pelagic food usually decreases markedly with increasing distance from the coast, and the amount reaching the bottom in areas of very deep water is further reduced by its disintegration while sinking. Hence, the littoral muds are most rich in food, and the red clay at great depths and far from shore is the poorest. This difference is reflected in the number of animals actually collected from different areas (cf. p. 806).

The Pelagic Environment and Its Subdivisions. The pelagic division includes all of the ocean waters covering the benthic division. Horizontally, the pelagic division is subdivided into an open-sea (oceanic) province, and an inshore (neritic) province.

Vertically, the *oceanic province* has an upper lighted zone and a lower dark zone with no well-marked boundary between the two. For convenience the boundary is arbitrarily set at 200 m, since this would correspond with the arbitrarily set depth for the edge of the continental shelf and at the same time place the littoral system and the neritic province in areas definitely within the lighted portion. Actually, light changes gradually in both quantity and quality from the very surface downward to depths where it is no longer detectable (p. 82), and this depth varies with latitude, season, amount of suspended material, living or dead, and therefore also with distance from shore. These variables of the pelagic environment are of profound importance to the population of the sea, as will be pointed out later.

The outstanding features of the oceanic province are the broad spatial expanses and the great ranges of depth. As distinguished from the neritic province the waters are as a rule very transparent, with little or no detritus of terrestrial origin. These waters are predominantly blue in color and support the blue surface fauna to be discussed more fully in chapter XVII. Although solar light penetrates relatively deeper than in inshore waters, the great depth of the water included in this province results in complete elimination of solar light in the deeper portion of the province, and as a result only carnivores and detritus feeders can exist in the very deep layers.

The chemical composition of the offshore water is relatively stable. Salinity is uniformly high, with only small fluctuations in space and time (p. 123), and plant nutrients are frequently relatively low in the upper layer and only slowly replaced.

The vertical border separating the *neritic province* from the oceanic is set at the edge of the continental shelf; hence all water of depths shallower than 200 m would fall within the neritic province, which accordingly may extend far seaward in instances where the continental shelf is broad, as off the east coast of the United States, or be very narrow, as off the west coast of South America.

Although biologically and chemically the border between the oceanic and the neritic provinces is not strictly definable, yet as we approach the coast the plant and animal life takes on characteristics not found in the typically oceanic province where "blue-sea" forms prevail. The chemical constituents of the sea water in the neritic province are more variable than in the oceanic. Salinities are usually lower, sometimes markedly, and undergo seasonal or sporadic fluctuations such that many of the inhabitants are more or less euryhaline in nature—that is, able to endure wide ranges of salinity. River water may bring in nutrients and may also exert a stabilizing influence on the turbulent motion, being at times, therefore, instrumental in initiating plant growth in the upper layers (p. 789). Plant nutrients, nitrates, phosphorus, and so on are more readily available in the shallower inshore water because of the greater possibility of return by vertical currents after they have been regenerated from the disintegrating organisms on the bottom or in the deeper water (chapter VII). This factor is of the utmost importance to production of diatoms, foremost of the primary food of the sea. Therefore, per unit area of the sea, the neritic province is far more productive than the oceanic province and is consequently the region of greatest importance to marine life in general. Here fish of greatest economic importance are taken, not only because of greater availability, but also because it is their natural habitat.

Other Biotic Units. The above classification of the marine environments is based mainly on broad geographical, physical, chemical, and biological characteristics that circumscribe more or less clearly the separate zones. Within each of these extensive zones we observe many and varied sets of ecological conditions resulting from differences in substratum, proximity to shore, depth and chemical-physical condition of the water, and so forth.

The primary "topographic" unit used in ecological classification of the environment is the *biotope*, or *niche*, which is defined as "an area of which the principal habitat conditions and the living forms which are adapted to them are uniform" (Hesse, Allee, and Schmidt, 1937). Since in any given type of biotope the habitat conditions make specific demands on the inhabitants, it follows that an analogous development of the inhabitants is frequently reflected in the population, and those not fitted for the habitat are eliminated from it. Obviously, some organisms are not so narrowly bound to the biotope as are others of more specialized nature. Thus, within a biotope may be found some generalized forms such as certain cephalopods and fishes that wander more or less freely from one type of biotope to another. The more specialized a biotope becomes with respect to living conditions, the more uniform will the inhabitants become, so that only a few species with large numbers of individuals may exist. The smaller habitat anomalies found within the biotope are called *facies*. The number of organisms that can live in any given biotope may in special cases be determined by available suitable space, but more frequently it will depend upon the food supply that may be produced within the biotope or be carried to it from outside by currents. The community of forms in a biotope is called a *biocoenosis*.

Biotopes having certain characteristics in common—for example, proximity to the coast or estuarine locality—are united into larger divisions known as *biochores*.

General Character of Populations of the Primary Biotic Divisions

Under the previous headings we have dealt with the classification of the marine *environment*. For purposes of future discussion it is desirable at this point to outline briefly a broad, highly practical classification of the marine *population* inhabiting the above primary biotic divisions, a classification based not on natural phylogenetic or taxonomic relationships, as given on p. 282, but rather on an artificial basis, grouping heterogeneous assortments of organisms depending upon common habits of locomotion and mode of life and upon common ecological distribution.

On these grounds the population of the sea may be divided into three large groups—namely, the benthos, nekton, and plankton, the first belonging to the benthic region and the other two to the pelagic region.

In the *benthos* (Gr., *deep* or *deep-sea*) are included the sessile, creeping, and burrowing organisms found on the bottom of the sea. Representatives of the group extend from the high-tide level down into the abyssal depths. The benthos comprises (1) sessile animals, such as the sponges, barnacles, mussels, oysters, crinoids, corals, hydroids, bryozoa, some of the worms, all of the seaweeds and eel grasses, and many of the diatoms, (2) creeping forms, such as crabs, lobsters, certain copepods, amphipods, and many other crustacea, many protozoa, snails, and some bivalves and fishes, and (3) burrowing forms, including most of the clams and worms, some crustacea, and echinoderms.

The *nekton* (Gr., *swimming*) is composed of swimming animals found in the pelagic division. In this group are included most of the adult squids, fishes, and whales—namely, all of the marine animals that are able to migrate freely over considerable distances. Obviously, there are no plants in this general group.

In the *plankton* (Gr., *wanderer*) is included all of the floating or drifting life of the pelagic division of the sea. The organisms, both plant and animal, of this division are usually microscopic or relatively small; they float more or less passively with the currents and are therefore at the mercy of prevailing water movements. Many of the animals are able to make some progress in swimming, although their organs of locomotion are relatively weak and ineffective. The plankton is divided into two main divisions, the *phytoplankton* and the *zooplankton*. The former comprises all of the floating plants, such as diatoms, dinoflagellates, coccolithophores, and sargassum weeds. In the zooplankton are included (1) myriads of animals that live permanently in a floating state, and (2) countless numbers of helpless larvae and eggs of the animal benthos and nekton. Since the plankton and nekton occupy the same biotic realm and are part of the same community, it is necessary always to remember that the distinction is one based primarily on relative size and speed of swimming, and does not signify a divergence of ecological relationship.

Each of these three ecological groups will be more fully discussed in later chapters.

Development of Life in the Sea

Let us review briefly the observations that indicate the relative antiquity of the marine environment as a biological realm. It is not possible to know when life arose in the sea, but the close similarity of the chemical composition of body fluids and sea water has led to the supposition that the sea was already saline at that early time and that, because of the intimacy of primitive organisms with the fluid environment, the elements present entered into the fundamental composition and mode of metabolism of the primitive organisms and are maintained in present-day forms with certain modifications in the proportions of the principal ions, especially magnesium (table 55). These interesting relationships have led to much speculation relative to the development of organisms and the chemical composition of primitive seas, but we cannot enter further upon that phase of the action of the environment. Pearse (1936) has given some reviews and listed literature pertaining to these questions and to the theory of migration of animals from sea to land.

The part played by the sea in the distribution and maintenance of present-day life upon our globe is a vital one. The sea itself is abundantly populated, and no life could exist on land were it not for the perpetual water cycle of evaporation, precipitation, and drainage between sea and land. Only in the sea would it be possible to approach any degree of self-sufficiency as a biological realm, and historically the sea has acted a principal role in the development of animal life.

That the sea is the original environment of animal life is strongly indicated by certain facts that point to the greater age of marine life as compared to terrestrial and fresh-water faunas to which it has seemingly given rise. Evidence pointing to a greater age of marine fauna over the terrestrial and fresh-water faunas is mainly along four lines: (1) general composition of present-day faunas, (2) similarity in the chemical composition of body fluids and sea water, (3) life histories, and (4) paleontological relationships.

(1) The whole animal kingdom is divided into a number of primary divisions, each known as a *phylum*. Each phylum is composed of animals having certain fundamental morphological similarities not possessed by any animals of other phyla. Thus, a natural, as opposed to artificial, relationship is indicated. Each phylum is then divided into natural but more restricted groups known as classes, and these in turn are followed by other yet lower divisions in the following manner:

Phylum
Class
Order
Family
Genus
Species

Species are formed of individuals, and the morphological features by which each species is characterized are less fundamental and presumably of more recent origin than those characterizing the genera. Similarly, the generic structures are less fundamental than those of families, and so on to the highest division, which is based on structures of great antiquity.

A review of all the higher or major divisions—namely, the phyla and classes of animal life—reveals the striking preponderance of marine groups. All of the seventeen phyla (using the taxonomic ranking of H. S. Pratt, 1935, in *Manual of Invertebrate Animals*) are represented in the sea, and most, if not all, are believed to have originated there. The following five are exclusively marine: *Ctenophora, Echinodermata, Phoronidea, Brachiopoda, Chaetognatha.* Some authors recognize fewer than seventeen phyla, but this has only the effect of increasing the preponderance of purely marine classes.

Of the forty-seven classes (where only subphyla were given under phyla, they are here rated as classes) of invertebrates as given by Pratt, twenty-one, or 43.7 per cent, are exclusively marine, and only three, or

6.2 per cent, are exclusively nonmarine. Of the subphylum Vertebrata, only members of the class Amphibia are nonmarine, while the other four classes share members in both marine and nonmarine environments. The fishes are predominantly marine, while the reptiles, birds, and mammals are predominantly terrestrial. The amphibians represent the highest nonmarine group.

These divisions demonstrate the astonishing variety of marine animals, as far as the major phylogenetic groups are concerned. However, the terrestrial environment harbors the greatest number of *species*, mainly owing to the large number of species of one restricted group, the insects, which are almost totally absent from the sea. The presence in the sea of so many major groups, many of which are restricted to the sea, indicates the great tendency on the part of the marine environment to preserve the groups that have once become evolved.

It should be noted also that, in addition to the remarkable diversity of marine life in the ocean, there is a conspicuous primitive element, as judged by simplicity of structure, in the groups represented. In the sea there is a more complete developmental series of animal life than exists anywhere else, because of which, and also because of the natural and intimate relationships of the organisms to the sea-water medium, the studies issuing from the marine biological laboratories have contributed vastly to information on biological problems dealing with development and maintenance of life.

The relative uniformity of the marine environment has been instrumental not only in preserving the diversity of forms but also in retaining a generally more primitive character as compared with terrestrial and fresh-water animals. It is true that in the sea we do find associated with the lower forms a number of highly developed animals that must be considered marine because of their dependence on the sea. These are the seals, whales, certain reptiles, fishes, and birds. All of these groups, however, have had a large part of their racial development in the terrestrial and fresh-water habitat. They have more recently reverted to the sea and have only secondarily become adapted to it. The teleost fishes, which are believed to have evolved to their present status in fresh water, were originally derived from marine stock.

(2) The relation of body fluids to sea water has already been discussed (p. 269).

(3) A study of the life histories of invertebrates suggests the antiquity of marine life. During the early history of the individuals of some animal groups the larval stages are markedly different in structure and habit from the mature phase. The larval stages, which sometimes resemble the mature stages of other groups or only the larvae of other groups, are thought to reflect a structural similarity to ancestral stock. Whether or not this is a real recapitulation of racial history or only an

expression of individual larval adaptation to a common environment is important in seeking an understanding of the similarity. Whatever the truth may be, it is well known that most marine invertebrates pass through an early stage during which the larvae in no way structurally suggest their parentage, but may even have striking fundamental similarity to existing larvae of other groups. From this it has been possible to establish types of larvae—for example, the *trochophore* of the Annelida and Mollusca, and the *nauplius* of the crustacean groups (fig. 80, p. 321).

There is a tendency for some aggressive animal groups to desert the sea for fresh-water or land habitats. This is shown by the crustaceans, among which there are forms such as the prawn, *Eriocheir*, which enters fresh water at a young stage but when mature returns to the sea to spawn. The land crabs, *Cardisoma*, *Gecarcinua*, and so forth, also go through a free-swimming larval stage in sea water.

(4) It is well known that animal fossils occurring in the oldest known fossiliferous rocks of the earth's crust are mainly marine forms.

Marine animals were abundant and became fossilized in the Cambrian period (500 million years ago), when certain portions of the land now above sea level formed a part of the sea bottom along the coasts of ancient seas. Several invertebrate phyla were already developed, and such forms as trilobites and brachiopods were particularly abundant.

The chief roles of the marine and terrestrial environments in the development of life may be summarized by saying that the great part played by the former is chiefly in the development and maintenance of a wide diversity of lower forms, while in the latter the influence of the more rigorous habitats has produced less diversity of form but a higher type of complexity.

The area where these two great environments meet, the intertidal zone, is in an intermediate position and subject to rapid and marked vicissitudes, and it is from here that much of the migration to land is supposed to have taken place.

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