THE BIOLOGY OF MARINE ANIMALS

by

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PREFACE

EACH YEAR many young biologists make an excursion to the sea, not on idle pleasure bent but for the purpose of studying and investigating marine organisms. For some of these visitors it is perhaps their first actual experience of marine animals in their natural environment, and they will be captivated but bewildered by the multiplicity of life and by the diversity of biological adaptations which they will encounter. It is for these young men and women and for undergraduates specializing in marine zoology that this book has been written, but it is hoped that lecturers and investigators in other fields may find some diversion, if not actual instruction, in the following chapters.

This book is concerned with the comparative physiology of marine animals, and a knowledge of comparative morphology and general biology has been presumed on the part of the reader. There are limited excursions into allied fields of animal behaviour and ecology, when these can be related to the main theme. In the pages which follow I have tried to show some of the manifold ways in which marine animals, from all kinds of environments, have been able to maintain themselves in the face of hostile physical conditions and severe biotic competition. Whenever possible, at the risk of prolixity, I have cited specific examples in the belief that the functioning and adjustments of each animal deserve particular consideration, as revealing how it has managed to solve certain problems of existence.

Only animals belonging to the marine environment are considered. Probably no apology is needed for this, since the ocean forms a remarkably stable and uniformly graded environment, with far less range of variation than that encountered on land or in fresh water. I have given some consideration to problems of littoral and estuarine ecology at the transition between sea, land and fresh water, and of animal associations, when these present features of particular interest to the marine zoologist. Of course, the great majority of examples are taken from littoral and inshore species, for these are the ones most readily available and therefore most thoroughly investigated.

This book has been in preparation for six years, and during that time many aspects have received extensive treatment elsewhere. Full bibliographies of earlier work in comparative physiology are now available and I have therefore confined myself principally to quoting works of the past two decades, including sources in which extensive reference lists may be found. Whenever possible I have attempted to use the presently accepted scientific name for each species mentioned, but there are undoubtedly many instances in which this goal has not been achieved. All measurements are given in the c.g.s. system.

During the preparation of this book I have received much assistance and advice from friends and colleagues. I am grateful to the following for reading certain chapters and for critical comments: Dr. W. R. G. Atkins, D. F. S. Russell, Professor C. M. Yonge, Dr. J. D. Robertson, Dr. D. Davenport, Dr. G. Y. Kennedy, Dr. H. W. Harvey, Mr. F. A. J. Armstrong and Dr. R. D. Keynes. Their criticisms and suggestions have done much to give the book any merit it deserves, but for the errors and egregious blunders which remain I reserve for myself full credit. Finally, I wish to acknowledge the great debt I owe to my wife for her encouragement and for assistance in preparing the text. She is also responsible for preparing many of the illustrations, which have been redrawn from the original sources.

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Plymouth, 1956

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CONTENTS

CHAPTER 1

INTRODUCTORY

> The sea, therefore, we may safely infer, has its offices and duties to perform; so, may we infer, have its currents, and so, too, its inhabitants; consequently, he who undertakes to study its phenomena must cease to regard it as a waste of waters. He must look upon it as a part of that exquisite machinery by which the harmonies of nature are preserved, and then he will begin to perceive the developments of order and the evidences of design; these make it a most beautiful and interesting subject for contemplation.
>
> LIEUT. F. M. MAURY, 1883

THE REALM OF MARINE LIFE

THE oceans in their vast expanses cover seven-tenths of the earth's surface and in their deepest reaches extend downwards into the earth's crust to some 10,000 metres below sea level. The mean depth of the ocean has been estimated at about 4,000 metres, which is considerably greater than the mean height of land above sea level, namely some 850 metres. All this tremendous expanse and depth are inhabited by living things; animals have been secured from beneath the polar ice sheets, and from the ocean deeps more than 10 kilometres beneath the surface. These abyssal forms are normal inhabitants of that world and know no other, and similarly at intermediate depths there are other animals which tend to remain at definite levels.

The ocean is not evenly populated throughout its extent. The density and total volume of living organisms are greatest in coastal waters and at the surface, and decrease rapidly with depth in the waters of the open ocean. The food of all animals in the sea is ultimately derived from marine plants, phytoplankton and, to a small extent, seaweeds. Since the energy for their synthetic activities is provided by sunlight, plants can thrive only in shallow or surface waters within the range of adequate light penetration. In these regions the herbivores graze upon the plants, but at deeper levels, extending down to the deepest waters of the abyss, the animals are dependent upon the remains of dead or dying surface organisms which slowly shower upon them from above, and to some extent upon the spatial organization of food chains in vertical series.

VARIETY OF MARINE ANIMALS

Of the nineteen or so phyla recognized by zoologists all except one or two are found in the sea. Of these, four are exclusively and four are predominantly marine in habit, while many of the remaining phyla are well represented. The entirely marine phyla are the Brachiopoda, Chaetognatha, Phoronidea and Echinodermata. Of the three most highly evolved groups of animals now extant, the molluscs, arthropods and vertebrates, all have marine representatives. The cephalopods are without doubt the most highly developed of marine invertebrates, and approach the vertebrates in the complexity of their sensori-neural organization and behaviour. Arthropods reached their evolutionary peak in the insects, few of which have returned to the sea. But more remarkable, from the historical viewpoint, has been the repeated re-invasion of the seas by most of the major groups of vertebrates. So successful was this colonization that the teleosts were able to exploit all marine environments from the tidal zone to the ocean abyss, and occupy a dominant position in the oceanic fauna. The maritime birds and mammals, partly through their acquisition of homoiothermism, have been able to spread through the surface waters of all the oceans from arctic to antarctic ice, and in speed and agility they even outclass the fish and squid in their own element. On the invertebrate animals hitherto occupying the seas the effects of these evolutionary changes have been tremendous. From our point of view they enter into a consideration of the morphological and functional adaptations which have permitted the exploitation of a marine environment.

MARINE HABITATS

On the basis of their distribution and habits marine animals are generally classified as plankton, nekton and benthos. The first-named comprises all those small drifting organisms, both plants and animals, which have only feeble powers of locomotion and are carried helplessly at the mercy of currents and tides. Nekton refers to strong swimming animals, such as squid, fish and whales, whose movements are powerful enough to make them independent of water movements to a considerable degree. And thirdly, the benthos embraces all those bottom-living organisms which crawl over the substratum, burrow into it, or are sedentary in habit and remain fixed to one spot, for example, starfish, bivalves and sponges.

In addition to this classification of marine animals on the basis of habitat it is usual to recognize certain well-defined environments in the sea, each with special characteristics of its own. These are the littoral or inter-tidal region, the continental shelf and slope, the pelagic zone and the abyssal region. Subdivision of these various regions is often necessary for oceanographical and ecological purposes, and is briefly described in the following paragraphs. More extended treatment will be found in works on marine natural history and oceanography, such as Sverdrup *et al.* (37), Coker (11), Colman (12) and Marshall (31).

The Inter-tidal Zone

At the junction between sea and land lies the shore or littoral zone, subject to tidal ebb and flow. This is the region bounded by extreme high- and low-water levels of spring tides. Its vertical range depends on the extent of the tides, and the area involved is also governed by the slope of the shore. Conditions of life in the littoral zone are quite dissimilar from those occurring elsewhere. When the tide is in the inhabitants are bathed by sea water, a relatively constant medium, but during tidal ebb they are periodically uncovered and exposed to the rigours of aerial climate. Quantitatively the fauna of the shore is very rich, but the vicissitudes of existence associated with this environment have led to a high degree of specialization. Consequently the population of the shore is peculiar in many respects and contains a high proportion of animals not found elsewhere. Because the littoral zone is more readily accessible to the zoologist than the waters offshore, and the animals living there can be observed directly, this region has received much attention.

In the tidal zone several environmental levels can be distinguished, determined by the degree of atmospheric exposure to which they are subjected. On the lower shore, lying below low-water neaps, there are long periods during neap tides when the shore is not exposed. Here live many sublittoral animals which can tolerate only limited exposure to the air. Other sublittoral animals invade the inter-tidal region during tidal flow only, or come inshore on occasion to spawn. Lying between the limits of low- and high-water neaps is a region which is covered twice daily by the sea, and which contains a rich fauna of typical inter-tidal species. Above high-water neaps there are long periods when the shore is exposed for days on end. The fauna of this region contains fewer species than lower levels, and many of these are restricted to higher regions of the shore. Consequently, zonation of animals is a conspicuous feature of the shore, and is illustrated in Fig. 1.1 depicting conditions on a rocky shore in New Zealand (30, 36, 43, 44).

The environmental variables which adult animals encounter in the inter-tidal zone, and which they endeavour to counter by morphological, physiological and behavioural means, are manifold and complex. No other region in the ocean presents such diversity of habitats and range of physical conditions as the inter-tidal zone. The variables with which we are concerned may be considered as follows.

Water Movements. In the littoral region water movements result from waves, swell and tidal action. In sheltered bays and estuaries such movements may be slight and gentle, but on rocky coast lines facing the open ocean the mechanical force of the waves is tremendous.

Animals living on wave-swept shores resist the destructive effects of wave action by suitable structural devices, and by modifications of form, or they actively seek shelter and cover. Acorn barnacles live cemented to rocks, chitons and limpets adhere firmly with their broad feet, and mussels attach themselves by strong byssus threads. Certain shore-fish, for example *Lepadogaster*, have their pelvic fins modified into strong suckers. Finally, the depressed or conical shape of littoral chitons and limpets offers minimal resistance to water movements.

Emergence. As the result of tidal movements animals on the shore are periodically exposed to air, either daily, or for longer intervals if they live

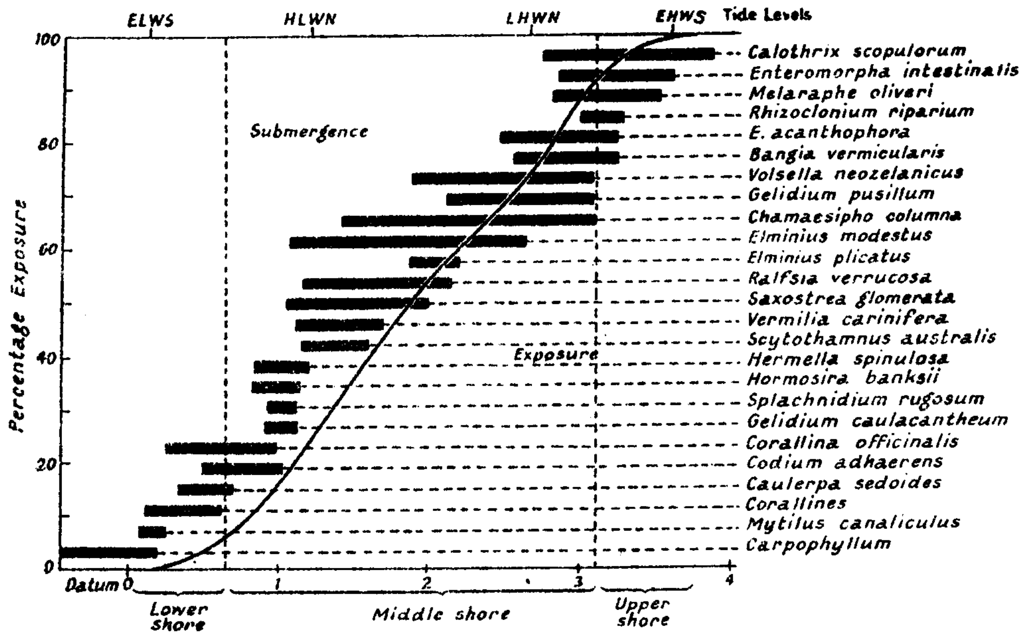

FIG. 1.1. ZONATION OF LITTORAL ANIMALS AND PLANTS ON A PROTECTED ROCKY SHORE (NARROW NECK REEF) IN NEW ZEALAND

Tide levels shown on the left: EHWS, extreme high-water springs; LHWN, lowest level of high-water neaps; HLWN, highest level of low-water neaps; ELWS, extreme low-water springs. Organisms at top. Algae, *Calothrix*, *Enteromorpha*, *Rhizoclonium*, *Bangia*, *Gelidium*, *Ralfsia*, *Scytothamnus*, *Hormosira*, *Splachnidium*, *Corallina*, *Codium*, *Caulerpa*, *Carpophyllum*. Polychaetes, *Vermilia*, *Hermella*. Molluscs, *Melaraphe*, *Volsella*, *Saxostrea*, *Mytilus*. Barnacles, *Chamaesipho*, *Elminius*. (After Dellow (16).)

above the level of high-water neaps (Fig. 1.1). Such animals may possess thick integuments which reduce the water lost through evaporation when the animal is in air (e.g. shore crabs) or hard shells which can be clamped firmly together during the period of exposure (e.g. shore barnacles and mussels). Still other forms obtain protection by burrowing into the substratum, creeping under rocks or into crevices, or among the fronds of shore-wrack, e.g. inter-tidal polychaetes and teleosts. The amount of exposure to the atmosphere which an animal can tolerate, and the pattern of its behaviour when the tide ebbs, are important factors governing its distribution on the shore.

Temperature. The inter-tidal zone experiences to a great degree the vicissitudes of terrestrial climate, and at low water animals are subject to the full range of aerial temperatures. Shore temperatures show great variation with latitude and season. On the shores of temperate regions ground temperatures may fall below 0°C in winter and reach 40°C in the heat of the summer sun, and higher temperatures will be encountered on tropical shores. Rock pools vary greatly in temperature, depending on their volume, on the air temperature and the length of time they are separated from the sea.

Littoral animals must of necessity be eurythermal in order to survive, and this is illustrated in investigations dealing with the heat tolerance of littoral gastropods. Broekhuysen (5) determined the lethal temperatures and the survival times at high temperatures for a series of shore gastropods at False Bay (South Africa), and he discovered that these factors were graded according to the zonal sequence of the species on the shore. Evans (20) has investigated the thermal death-points of littoral gastropods in Cardigan Bay. Mean lethal temperatures varied from 46·3°C for *Littorina neritoides* which lives above mean high-water neaps, to 36·2°C for *Gibbula cineraria* which occurs in damp shaded positions below mean low-water neaps. The highest temperatures recorded on the shore were 40·5°C for sun-baked rocks and 30°C in tidal pools. Both workers concluded that the degree of heat tolerance shown by these various snails is related to the temperature range which they encounter in nature, and the safety factor is sufficiently high so that they rarely, if ever, are exposed on the shore to temperatures that are lethal.

Abnormal temperatures may occasionally exceed the extremes tolerated by the species and result in considerable mortality. Few cold-blooded invertebrates have any means of opposing thermal fluctuations apart from seeking shelter. An interesting exception is the littoral isopod *Ligia* which has a temperature significantly below that of the environment in full sunlight, owing to the effect of evaporation of water vapour from the surface of the body. It has been suggested that such animals may migrate from enclosed humid niches in which the air is still, upwards into the open, where convection and evaporation can reduce the body temperature (17, 18). Also, there are some shore crabs which blanch when illuminated, and thereby reflect more of the incident light and heat. When these crabs are exposed on the shore this mechanism would tend to reduce the liability to heating in sunshine.

Salinity. Large variations in salinity occur in the inter-tidal region and in estuaries. During low tide the shore may be washed by rain water and those animals that are active and remain in the open may be surrounded by water which is almost fresh until the return of the sea. Freshwater seepage on the shore forms areas of reduced salinity, and these are favoured by certain species. Tidal pools are subject to considerable fluctuations in

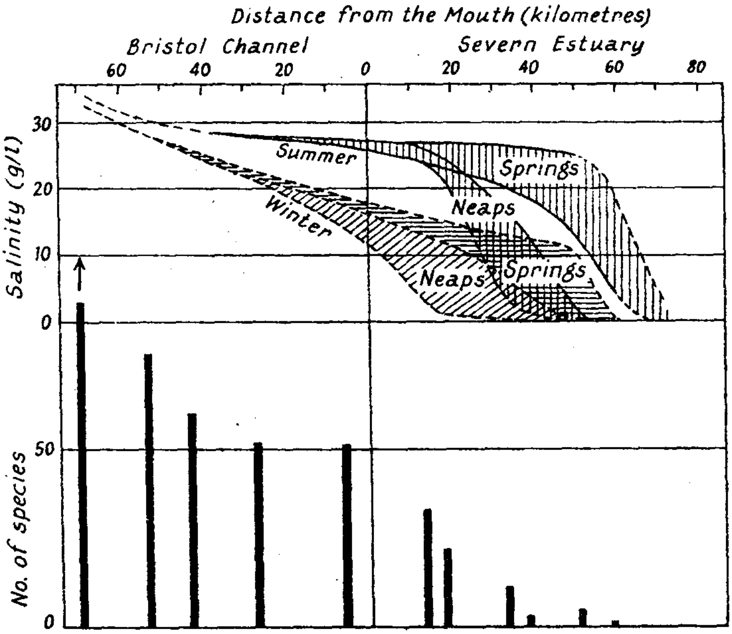

FIG. 1.2. SALINITY CHANGES IN AN ESTUARY (SEVERN), AND THE DECREASE IN THE NUMBER OF MARINE INTER-TIDAL ANIMALS AWAY FROM THE MOUTH

(*Above*) tidal and seasonal changes in salinity in the Bristol Channel and Severn Estuary (1940). (*Below*) number of species of marine inter-tidal animals recorded at various stations. (After Bassindale (4).)

salinity, particularly those pools high on the shore which are cut off from the sea for some days during the period of neap tides. Wide environmental variations in salinity demand tolerance or functional methods of regulation against osmotic stress, and these will be considered in the next chapter.

In estuaries the salinity conditions are peculiar owing to the effects of tidal oscillations and river discharge, leading to variable admixture of fresh and salt waters. Only a restricted number of marine animals can exist under such conditions of reduced and variable salinity, and it is found that the number of marine species decreases as the estuary is ascended (Fig. 1.2). The distance which any given species can penetrate up the estuary depends on the lowest salinity it can tolerate for a given time. For fixed or sedentary animals such as molluscs, this is determined by the lowest salinity at springs during the season of maximal run-off. Active and migratory animals such as shrimps, however, are able to execute seasonal movements up and down the estuary, moving towards the mouth in winter and upstream during the spring and summer (4, 23, 29, 44).

The Sea Floor

Below low-tide mark the sea floor slopes gently at first across the continental shelf to the continental edge at about 200 metres. The gradient then increases and the floor falls off rapidly down to a depth of around 4,000 metres. This region of sharp descent is the continental slope below which the floor tends to level out again as the abyssal plain. The continental shelf has an average width of about 50 kilometres, but the actual extent varies widely in different parts of the world. In certain areas, such as the Grand Banks of Newfoundland and the North Sea, the shelf extends several hundred kilometres offshore, whereas off steep coasts, such as Spain and Chile, it is only a few kilometres wide. The abyssal plain is far from even, and presents great depressions and ridges; the greatest depressions, called deeps, extend down to 10,500 metres.

Pelagic Zone

The pelagic zone comprises the waters of the open ocean, and because of its volume, expanse and the density of its population, it forms the major oceanic environment which the biologist has to consider. It is sometimes divided into three horizontal regions on the basis of light penetration in the following manner.

1. An upper photosynthetic zone in which the light intensity is sufficient to provide plants with energy for growth. This will vary in depth according to the amount of light falling upon the water, and with the transparency of the water. In clear tropical oceanic waters the photosynthetic zone will extend down to some 100 metres, but will be less elsewhere. This region is often rich in plankton and herbivorous animals.
2. A twilight zone extending below the photosynthetic zone to the limit of light penetration.
3. An aphotic zone extending from the limit of light penetration to the sea bottom. This region is dark, without living plant life and is populated solely by carnivorous animals and detritus feeders.

Planktonic Organisms. The most important members of the phytoplankton, upon which all pelagic animals are ultimately dependent for food, are the diatoms, followed by dinoflagellates. These plants can flourish only in the photosynthetic layer and, correspondingly, zooplankton is densest near the surface and diminishes with depth. The character of the plankton also changes qualitatively as well as quantitatively in hauls from deeper waters, surface species giving way to mesopelagic and bathypelagic forms. The quantity of zooplankton in surface waters also shows great geographical variation, becoming more abundant over the continental shelf and in higher latitudes. In general there is a tendency for a few species of planktonic animals to predominate in catches made in far northern and southern waters, but these occur in immense numbers. In tropical waters, on the other hand, the population density is low but there is great diversity and richness of species.

In temperate and sub-polar waters there is a rich seasonal growth of nutritive phytoplankton which in turn regulates the abundance of planktonic animals. Around the British Isles the seasonal increase in plankton first becomes noticeable between February and March as a rapid blooming of the diatom pasturage. This is followed in April by the hatching of

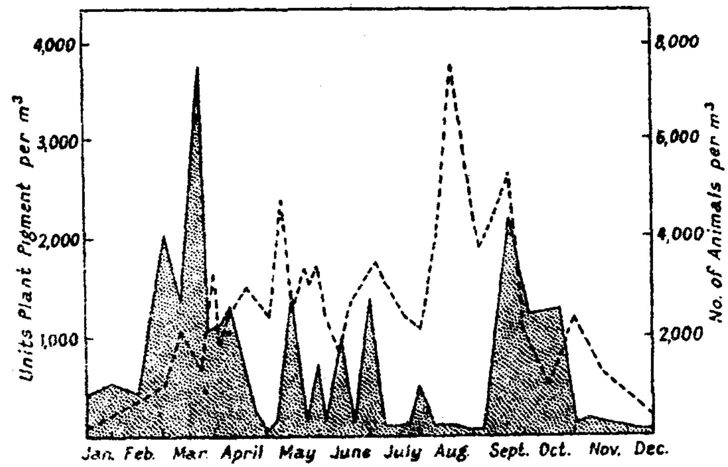

FIG. 1.3. GRAPHS SHOWING THE ANNUAL VARIATION OF PHYTOPLANKTON AND ZOOPLANKTON IN THE ENGLISH CHANNEL (1934)

Continuous line, phytoplankton; broken line, zooplankton. (From Harvey, Cooper, Lebour, and Russell (28).)

vast hordes of planktonic animals which batten upon the phytoplankton. Owing to the depletion of nutrient salts and the grazing effect of planktonic animals, the plants decline in abundance. A second minor outburst of phytoplankton may follow in the autumn (Fig. 1.3). During the winter months the plankton content of the surface waters sinks to a low ebb. In arctic and antarctic waters there is only a single annual outburst of planktonic life, in the summer.

The permanent members of the zooplankton are animals such as foraminifers, copepods, euphausiids, siphonophores, ctenophores, salps, chaetognaths, pteropods and so on, which spend all their life adrift. These are the holopelagic forms. In coastal waters another element comes into prominence, namely the temporary plankton. This embraces the drifting larval stages of numerous littoral and benthic species such as polychaetes, decapod crustacea, echinoderms and molluscs. With these should be included young stages of fish and cephalopods. The temporary members of the plankton attain great abundance during the spring and summer, only to disappear after metamorphosing, settling on the bottom or perishing. In addition there are certain temporary planktonic forms which are characteristic of the open ocean, such as the Phyllosoma larva of the rock lobster *Scyllarus*, and the Leptocephalus larva of the eel.

CHEMICAL AND PHYSICAL PROPERTIES OF SEA WATER

Physical and chemical conditions in the oceans have been investigated actively since the voyage of the *Challenger* in 1872–6, and extensive data are at hand for forming an appreciation of sea water as an environmental medium for animal life. The environmental variables which are of immediate interest to the biologist are temperature, density, viscosity, pressure, light, salinity, suspended matter and dissolved gases. These are briefly reviewed in the following pages and are related, in so far as is practicable, to their biological effects.

Chemical Composition of Sea Water

Sea water contains a characteristic assemblage of dissolved solids and gases, and a variable amount of suspended inorganic and organic material. As first shown by Dittmar on the *Challenger* expedition samples, the main constituents of sea water, with minor exceptions, show remarkable uniformity throughout the oceans of the world. This fact is of fundamental

TABLE 1.1

AVERAGE COMPOSITION OF SEA WATER (CHLORINITY 19‰, SALINITY 34·325‰)

Ion	Composition % of sea salt	Concentration g/kg of sea water	Concentration mM/kg	Concentration g/l. at 20°C (S.G. 1·024)
Na^+	30·61	10·556	459·02	10·809
K^+	1·10	0·380	9·72	0·389
Mg^{++}	3·69	1·272	52·30	1·303
Ca^{++}	1·16	0·400	9·98	0·410
Sr^{++}	0·04	0·0085	0·15	0·013
H_3BO_3	0·07	0·026	0·42	0·027
Cl^-	55·04	18·980	535·30	19·435
$SO_4^{=}$	7·68	2·649	27·57	2·713
HCO_3^-*	0·41	0·140	2·29	0·143
Br^-	0·19	0·065	0·81	0·067
F^-	0·004	0·001	0·05	0·001

* Bicarbonate and carbonate will vary according to the pH of the sea water.

importance in oceanography and marine biology, since it ensures that the results of studies on the physical properties of sea water in any part of the world are of general and universal significance. Table 1.1 shows mean values for the principal dissolved substances in sea water of chlorinity 19‰[1] (salinity 34·325‰).

[1] See p. 10 for explanation of ‰.

Since the major constituents of sea water retain the same relative proportions wherever the sample is taken, it is possible, by determining the concentration of any one of them, to estimate the concentrations of the others. Because of this constant composition the relations between chlorinity, salinity, density and temperature are fixed, and interconversion of values is readily carried out. Finally, the biologist recognizes, in the constant ionic composition of sea water, a stable environmental factor of the utmost importance in the physiology of marine animals.

The constancy in composition of sea water is due to the system of oceanic circulation and to the continual mixing which occurs. This soon equalizes any local variations resulting from the discharge of rivers, the activity of living organisms, formation and melting of sea ice, the interaction of suspended material with dissolved substances and exchange with bottom deposits. There are, however, restricted areas, such as the Black and Baltic Seas and the mouths of large rivers, where dilution and peculiarities of circulation bring about changes in the relative concentrations of dissolved substances. In such regions modifications of the chlorinity ratios with respect to sodium, potassium, calcium and sulphate ions may be encountered.

Salinity. The salt concentration of sea water is known as salinity. Salinities are always expressed as grammes per kilogramme of sea water (parts per mille, ‰) and, in practice, are usually obtained by measuring the chlorinity, using argentometric titration. The reader will find a simplified procedure in Harvey (25). The relationship between the two quantities, salinity and chlorinity, is given by the expression—

$$\text{Salinity (‰)} = 0{\cdot}03 + 1{\cdot}8050 \times \text{chlorinity (‰)}$$

For most biological purposes, the concentrations of substances in solution are usually expressed on a volume basis as percentages or grammes per litre. It is convenient, therefore, to have corresponding values for chlorine content, and this is available in the use of the term chlorosity, which is the equivalent of chlorinity expressed as grammes per litre at 20°C. The calculations involved are—

$$\text{molarity of Cl in sample} = \frac{(\text{vol } AgNO_3)\ (\text{molarity } AgNO_3)}{\text{vol sample c.c.}}$$

$$\text{chlorosity} = 35{\cdot}5\ (\text{molarity Cl})$$

$$\text{chlorinity} = \frac{\text{chlorosity}}{\text{density of sample at } 20^\circ\text{C}}.$$

The chlorinity may be read from the graph shown in Fig. 1.4 relating it to chlorosity, or may be calculated with greater accuracy from the data given in Knudsen's hydrographical tables.

The salinity range in the open oceans is rather small, and usually lies between 33‰ and 37‰ in surface waters, with a mean of nearly 35‰. Marked deviations from these values are due to peculiar conditions. In regions where there is much dilution by heavy rainfall, discharge of rivers