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Elizabeth M. Wood
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Introduction

By the nineteenth century, interest in the natural history of the seashore around the British Isles had been awakened, and explorations were also being made into coastal and offshore waters. Nets had long been used in open water for the capture of fish, but it was not until 1828, when a fine-mesh tow net was first used by amateur naturalist J. Vaughan Thompson, that the study of planktonic organisms really began.

At around this time, the piece of equipment most readily available for studying the benthos was a simple dredge consisting of a bag of coarse netting held open on a rectangular iron frame. Edward Forbes began dredging in British waters in 1840, and his pioneering work was taken up with great enthusiasm by other marine naturalists and scientists. By the end of the 19th century several marine laboratories had been established, and as time progressed, sampling techniques became more refined, with emphasis being laid on collecting quantitative data. This was possible with the study of planktonic organisms and the biota of soft substrata, but was less easy to achieve in rocky areas.

The first detailed *in situ* observations in the shallow sublittoral zone of the British Isles were made using standard (helmet) diving apparatus. The best known study is that by Kitching and his associates of a subtidal gully at Wembury in Devon (Kitching *et al.*, 1934). The cumbersome gear used at that time was far from ideal, and it was not until the invention of the aqualung that shallow coastal waters became more easily and directly accessible to man. Even then, in the late 1950s, diving was carried out more for the sense of adventure than for any other reason. However, it was not long before the potential of the equipment was realized and serious biological work began. Now, *in situ* studies using the aqualung are recognized as an invaluable and essential part of many marine biological investigations, especially in rocky areas where work using more conventional techniques is not easy. Even so, the use of diving as a method of study has obvious limitations, not least of which are the need to avoid long, deep dives and the practical difficulties of working under cold, turbid, current-swept and other inhospitable conditions.

Despite the drawbacks, a great deal has been learnt by diving biologists in the last twenty years or so about the ecology of the sublittoral zone and the behaviour and interactions of the organisms living there. This information, linked with data obtained from remote sampling and recording programmes, and from laboratory research, provides an increasingly detailed picture of the subtidal environment of the British Isles and its inhabitants. It is the essence of all these aspects that is conveyed in this book.

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The Sublittoral Environment

2.1 Coastal and sea-bed topography

The sublittoral zone includes the whole of the continental shelf, from the low tide mark to depths of around 200 m. The subtidal is considered here as synonymous with the shallow sublittoral, which is generally regarded as the area between the low tide mark and around the 50 m depth contour. In some areas, particularly in the west and south-west, this contour is only a few hundred metres from the shore, but more frequently occurs several kilometres away. In the eastern Irish Sea and the central and southern North Sea the sea-bed shelves extremely gently and the 50 m contour is not reached for 100 km or more. The southern North Sea in particular is relatively shallow over a wide area, although there are deeper pockets in places (Fig. 2.1).

Coastal and sea-bed topography are two important factors that determine the biological nature of benthic marine ecosystems. In this context nearshore ecosystems show more complexity than offshore ones because of the way physical features of islands or mainland modify the environment. Many nearshore areas lie along open coastline, but others are slightly, partially or completely enclosed by land and in western Scotland in particular, where the coastline is indented and there are numerous islands, many open-ended channels are formed. Narrow inlets (rias) occur in south-west England and Ireland. Some are small, but one of the largest, at Milford Haven, penetrates more than 20 km inland. A typical ria is steep sided, with strong tidal currents at the entrance, but little diluted by freshwater. Sea lochs are more enclosed than rias, and the outlet to the sea is comparatively small in relation to their overall size. Fast tidal streams sweep through the loch entrance, and conditions in these rapids contrast with the much stiller conditions found at the head of the loch. Incomplete interchange of water between loch and open sea may lead to brackish conditions in the enclosed area.

Coastal lagoons are cut off from the sea by low-lying banks of sand or shingle and water movement tends to be minimal. Lagoonal waters are seldom uniformly saline and there may be areas of reduced or increased salinity away from the entrance to the sea. Estuaries differ from lagoons in that they have a relatively open mouth and a considerable input of freshwater at the landward end. There is typically a wide range of salinities, and often distinct horizontal and vertical salinity gradients. Intermediate between lagoons and estuaries, and combining features of both, are semi-enclosed bays. In these areas accretion and

Fig. 2.1 Sea areas and depth contours around the British Isles. Adapted partly from Lee and Ramster (1981).

erosion of mobile sediments is a continual process, and illustrates the dynamic nature of these parts of the coastline.

2.2 Nature of the sea-bed

The sea-bed around the British Isles is far from uniform; its nature determined by the immediate underlying geological structure, and the amount and type of deposited material. Soft, sedimentary bedrock such as chalk and boulder clay, characteristically found in south-east England, tends to erode rapidly underwater and produce a fairly flat, unstable sea-bed. Thus the striking cliffs at Brighton, Dover and Flamborough Head are not matched underwater but continue as low-lying bedrock or boulder reefs. Limestones and sandstones occur right round the British Isles and are also sedimentary rocks, but are harder and less prone to erosion. However, all are laid down in layers, and the different strata erode at different rates according to their hardness and orientation. In this way reefs, ridges and cliffs are formed underwater and often show secondary erosional features such as caverns, crevices and ledges. Granite, basalt and other hard, igneous rocks from the immediate sea-bed off much of south-west Britain, Scotland and Ireland, and in places give rise to spectacular pinnacles, stacks and steep cliffs underwater. These rocks may erode and split along natural faults, but their hardness prevents them from becoming highly fissured.

In many areas the sea-bed is covered by deposits such as mud, sand, gravel or shell remains, which can cover the underlying bedrock by a few centimetres or many metres. These deposits may occur in localized pockets such as sheltered gullies or bays, or extend over large areas to form sublittoral plains. The gross distribution of mobile deposits around the British Isles is dependent on the action of currents and waves on material deposited over a period of many thousands of years (Fig 2.2).

Mobile deposits continue to be fed into the sea from the land, and a further source of sediments is from the erosion of coastal and marine rocks. For example Devonian slates off the Devon and Cornwall coasts contribute shaly materials to inshore deposits, and these finally break down to silt and clay. In a similar way, there is renewal of sands from the break-up of shells. Calcareous materials are present in nearly all deposits, and often accumulate to form characteristic shell gravels consisting mainly of bivalve shells, such as *Glycymeris*. Coralline gravels may also be formed, for example from the remains of the coralline alga *Lithothamnion calcareum*. Finally, there is a continual input of sediments in the form of organic debris from faecal material and the decay of dead organisms, both in the water column and on the sea-bed.

As a consequence of sorting, mud and fine sand has accumulated on the floor of the North Sea and, locally, has built up in estuaries, lagoons, harbours, deep offshore pockets, and other sheltered places where there is very little water movement (less than about 5 cm sec^{-1}). In contrast, where water movement is strong (i.e. more than 100 cm sec^{-1}) pebbles, shale, shell gravel, sand and other coarse materials are scoured from the sea-bed, leaving exposed bedrock. This has happened in particular off western coastlines. It has also occurred in the central part of the English Channel, where much of the sand originally available for redistribution following the post-glacial rise in sea level has been transported westwards by currents of 160 cm sec^{-1} or more (Holme and Wilson, 1985). In many parts of the English Channel there is only a thin veneer of sediment, about 10–15 cm deep, overlying the rocks. The sea-bed in parts of the Bristol Channel that experience current speeds greater than 3 knots (156 cm sec^{-1}) consists of rocks and boulders that have been worn smooth by the tidal scour. As the current slackens gravel begins to accumulate, especially in hollows in the bedrock, and small gravel waves may be formed (Warwick and Davies, 1977). At current speeds of 1.5–2.5 knots (78–130 cm sec^{-1}) sand

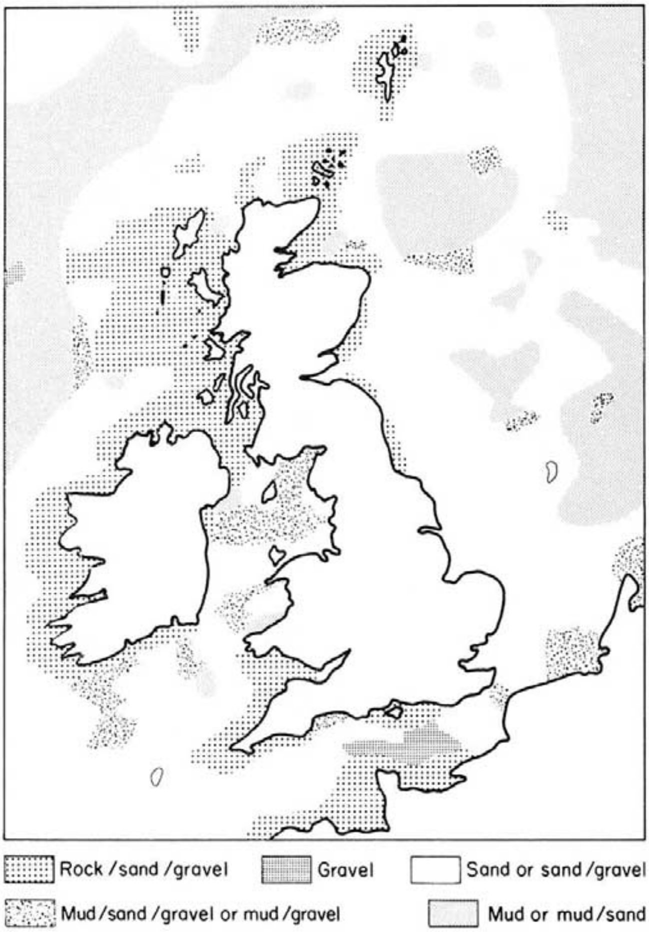

Fig. 2.2 Characteristics of the sea-bed around the British Isles. Adapted from Lee and Ramster (1981).

ribbons a few centimetres thick occur, while at lesser speeds large sand waves are formed. In areas where currents are weak, fine to muddy sand is deposited.

2.3 Patterns of water movement

2.3.1 Ocean currents

The greatest influence on gross patterns of water flow around the British Isles stems from the Gulf Stream, which originates in the western Atlantic Ocean. The main thrust of this current circulates down to the west coast of Africa, but a northerly offshoot, the North Atlantic current, is deflected upwards towards the Bay of Biscay. It eventually reaches western and northern coastlines of the

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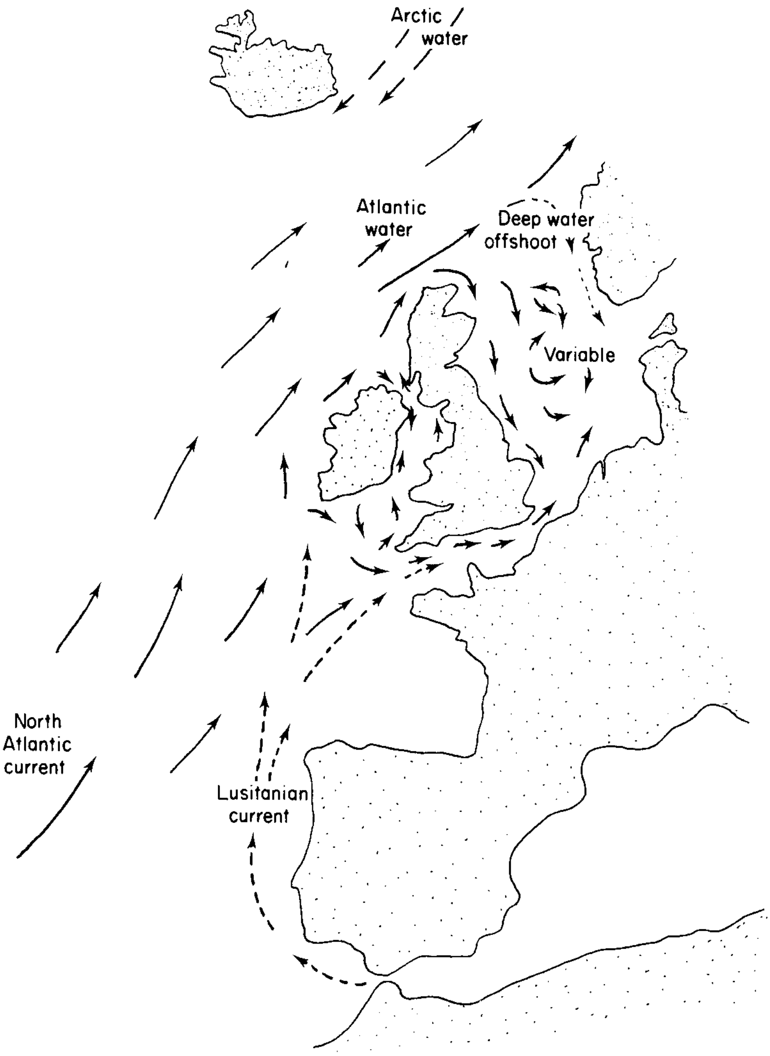

Fig. 2.3 Major patterns of water movement around the British Isles.

British Isles where it is known as the North Atlantic drift (Fig. 2.3). Another source of warm water is the Lusitanian or Mediterranean current. This has a deep outflow from the Mediterranean and gradually moves towards the surface, joining the North Atlantic drift current and finally upwelling off the west coast of the British Isles. There is a steady residual flow of water into the southern North Sea from the English Channel and slight penetration into the northern North Sea by the North Atlantic drift. Currents in the central North Sea are variable and essentially wind-driven, and the main outflow from the North Sea is along the Norwegian coast to the north.

2.3.2 Tidal currents

Coastal waters of the British Isles experience relatively strong tides originating from tidal movements in the North Atlantic Ocean which are magnified as they reach the continental shelf. Particularly strong tidal streams occur where water is funnelled through channels such as the Dover Straits or the entrances to the Irish Sea. Localized tide races flow around headlands or promontories and through narrow gaps between rocks and islands. In these situations flow rate generally reaches 2–3 knots (104–156 cm sec^{-1}) and may be as high as 5 knots (260 cm sec^{-1}). In the Bristol Channel, where the water is pushed forward into an ever narrowing space, tidal streams approaching 7 knots (364 cm sec^{-1}) are experienced. Smaller inlets on western and south-western coasts experience similar small scale surges, and tidal streams up to 8 knots (416 cm sec^{-1}) may occur in the entrance to sea lochs. In most of the North Sea tidal streams up to 3 knots (156 cm sec^{-1}) are possible, but in general they do not exceed 1 knot (52 cm sec^{-1}).

Superimposed on this overall picture are variations produced at a local level which are not indicated on bathymetric charts. Tidal currents may be reduced, deflected, accentuated or in some other way altered by small scale topographical features of the sea-bed, and these changes have an impact on sublittoral communities.

2.3.3 Waves

Waves are generated by winds blowing across the surface of the water and their size depends on wind speed, length of time the wind prevails, and the distance over open water the wind has blown (fetch). Coastal areas facing west are exposed to the open Atlantic and, in the case of prolonged storms, could be subjected to waves with a height of up to 35 m. Maximum wave height off the central east coast does not exceed 20 m, while in the south-east it remains below 10 m, even under severe conditions (Lee and Ramster, 1981). Average wave height is, of course, less extreme, but the general pattern still remains, though modified by topographical features of the coastline and the sea-bed.

Surface waves travelling over deeper areas of the continental shelf have no direct physical impact on the sea-bed. This is because the orbital motion created on the surface diminishes logarithmically with depth and has died away before it reaches the bottom. The situation is different in the coastal fringe, where the sea-bed may be consistently or periodically affected by wave-induced water movement. Waves are felt to a depth approximately equal to their wave length, but their motion is modified by both the presence and slope of the sea-bed.

Another characteristic of waves is that as they approach the shore they are deflected towards it as a result of refraction. One outcome of this is that their impact is spread disproportionately along the coastline, according to coastal features. The energy of the wave front becomes concentrated on headlands and promontories whilst it is correspondingly diminished in bays. In coastal areas where the sea-bed is rocky and uneven there may be further modifications in the

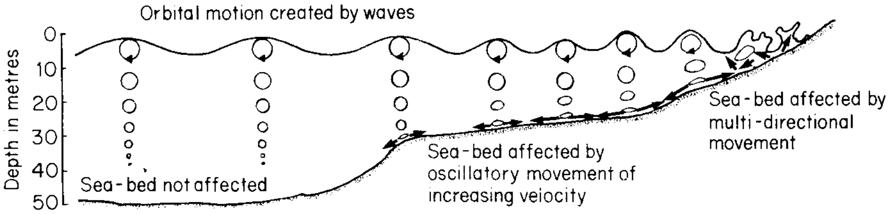

Fig. 2.4 Simplified illustration of the changing effect of surface waves of moderate strength on a sloping sea-bed. Modified from Riedl (1964), and Hiscock (1983).

degree of exposure to wave action. In this way reefs and pinnacles of rock can cause very localized variations in water movement from the lee side to the exposed side.

2.4 Temperature

The temperature of coastal waters around the British Isles varies according to geographic location, season and depth. The south-west is consistently warmer throughout the year while the central east coast experiences not only the coldest temperatures but also the widest fluctuations. This pattern is determined by the overall gradient of ambient temperatures from north to south, the warm water currents flowing along western coastlines and the influence of the continental land mass to the east. It is modified on a local scale by factors such as inflow of river water and patterns of water movement (Fig. 2.5).

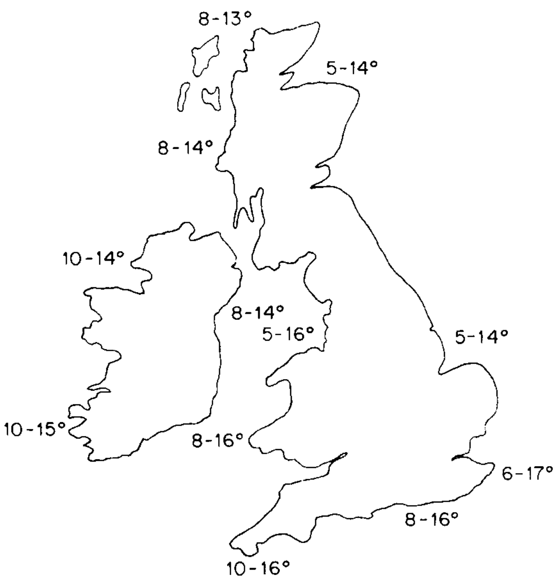

Fig. 2.5 Variations in mean surface temperature (°C, winter–summer) around the British Isles. Based on information in Lee and Ramster (1981).

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Vertical layering (stratification) may occur in certain areas, but the extent to which this happens depends on the amount of heat falling on the surface of the sea and the degree of mixing which subsequently takes place. Warm water is less dense and remains at the top of the water column unless disturbed and mixed by water movements. In winter there is little or no temperature stratification in the shallow sublittoral, and in spring and summer the temperature of surface waters in many areas is only a degree or two higher than it is at 40–50 metres. However, in areas where there is relatively little mixing, a well-defined interface (thermocline) develops in the spring and summer months. A sudden drop of several degrees is experienced over just a few metres, dividing the water column into a warm upper zone, and an underlying layer not directly affected by the sun's rays.

Horizontal discontinuities have also been discovered in recent years, although the temperature difference between the two adjacent bodies of water is much less marked than it is at the thermocline. However, a temperature change of 1 °C per kilometre may occur across the boundary zone known as the 'front'. These fronts tend to form roughly in the same areas each year, and are particularly evident where oceanic waters meet coastal waters (Fig. 2.6). For example one appears in the western Irish Sea during the summer, marking the boundary between stratified offshore waters and mixed inshore waters.

2.5 Light

The behaviour of light when it reaches the surface of the sea, and again as it

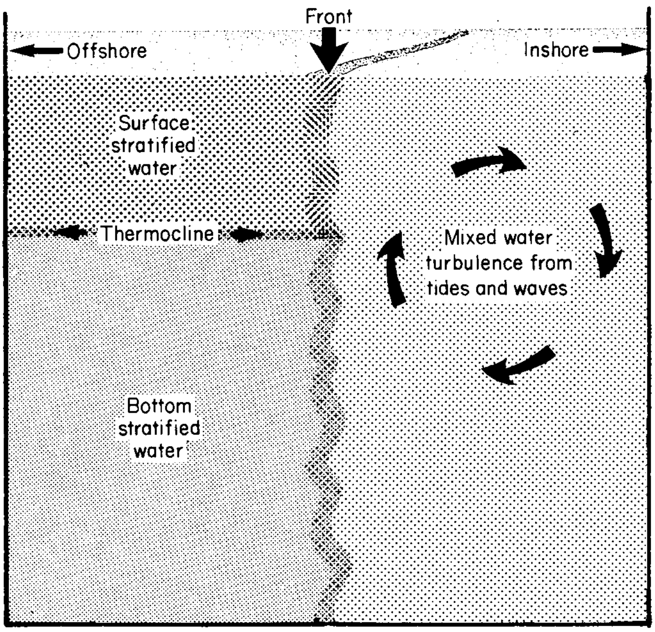

Fig. 2.6 Diagrammatic representation of a frontal system.

passes through the water column, is a complicated one. In the British Isles the intensity of incident light varies considerably with season, latitude and time of day, and is also affected by cloud and atmospheric conditions. Some or all of the light falling on the surface of the water is reflected away, unless the sun is directly overhead and the sea completely calm. Light that penetrates the water is then absorbed or scattered, but the rate at which this happens depends on turbidity and the type of particulate matter present. In westerly areas the sea-bed at 50 m may be clearly illuminated while in the North Sea, where turbidity is consistently high, it may, under optimal conditions, be only dimly lit at 10 m. Locally, a plankton bloom in surface waters or an inflow of silty river water can act as an effective barrier and prevent light reaching the sea-bed. Illumination is often significantly reduced in rocky areas where cliffs and overhangs cause shading, but in sandy areas illumination may be enhanced by reflection from the sea-bed. The quality of light is also affected because different wavelengths are absorbed at different rates. Coastal waters around the British Isles contain green and yellow pigments from phytoplankton and the products of organic decay, and blue light is selectively absorbed, resulting in a general green cast. The colour of the sea becomes bluer as turbidity decreases and the water becomes cleaner, a condition seldom seen at the eastern end of the English Channel or in the North Sea.

2.6 Salinity

Western approaches are influenced by water originating from the Atlantic Ocean and salinity is normally around 35 ‰ (parts per thousand), but in much of the North Sea the level is held down to around 34 ‰ because of dilution by river water. Even lower levels are found in the eastern Irish Sea. Marginal changes in this overall pattern occur between winter and summer and between surface and bottom waters, but the most marked differences are found in enclosed or semi-enclosed waters. Freshwater inflow depresses the level of dissolved salts, while evaporation causes it to rise, and salinity is determined by these and other factors, such as the degree of tidal flushing. The salinity regime in estuaries is particularly complicated and there are horizontal as well as vertical gradients which fluctuate with every tide. In enclosed or semi-enclosed coastal areas with a freshwater input isoclines may develop in parallel with thermoclines, marking a discontinuity between less saline surface water and denser bottom water.

2.7 Gases, nutrients and organic material

Atmospheric gases enter into solution across the sea–air interface, and well-mixed surface layers above the thermocline have a uniformly high dissolved gas content. In well-lit areas where photosynthesis is taking place the percentage saturation of dissolved oxygen may exceed 100%. In deeper areas, and especially below the euphotic zone, oxygen levels tend to be lower because there is no direct input from photosynthetic processes, yet oxygen is being used during respiration of bacteria and other organisms. Where water becomes stratified